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Exploring Behavior and Social Relationships of a Captive Group of Chimpanzees *(Pan troglodytes)*

Crystal E. Anderson
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To the Graduate Council:

I am submitting herewith a thesis written by Crystal E. Anderson entitled "Exploring Behavior and Social Relationships of a Captive Group of Chimpanzees *(Pan troglodytes)*." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Arts, with a major in Psychology.

Richard Saudargas, Major Professor

We have read this thesis and recommend its acceptance:

Gordon Burghardt, Debora Baldwin

Accepted for the Council:
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Graduate Studies

EXPLORING BEHAVIOR AND SOCIAL RELATIONSHIPS OF A CAPTIVE GROUP OF CHIMPANZEES (*Pan troglodytes*)

A Thesis
Presented for the
Master of Arts Degree
The University of Tennessee, Knoxville

Crystal Elizabeth Anderson
December 2005

DEDICATION

This thesis is dedicated to my family for their unwavering support, guidance, and love. They have been my inspiration, guiding me through this journey.

Life is made to give and not to take, for it is in giving
that we truly receive. As we receive the true
knowledge which is inherent within us,
that knowledge is used wisely in service.
---Gururaj Ananda Yogi

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ABSTRACT

An observational study was conducted on a captive group of chimpanzee, *Pan troglodytes,* to determine the overall behavior patterns, social organization, grooming relationships, and enclosure usage. Adolescence is a very dynamic time for young males and new group dynamics were expected to occur. The aim of the study was to investigate any shifting of social bonds among the group members and changes in the ranks of the two adolescent males. The two adolescent males (Lu and Mugsy) should have been demonstrating dominance behaviors towards the females, towards each other, and exhibiting sexual behaviors. Due to the unique group composition and the hand-rearing/peer-rearing background of the males, this study also attempted to assess if the males of the group expressed species and sex-specific behaviors characteristic of healthy, socially capable male chimpanzees. A variety of behaviors were examined to determine interindividual relationships and to predict which male will be the next alpha individual; however, due to the low frequency of occurrence of dominance and submissive behaviors, proximity and grooming data were the primary behavioral measures.

The data revealed that the males did not exhibit behaviors characteristic of their age and sex. The group remained in a stable state throughout the observation period with no observable status striving behaviors. Overall activity levels were low, with each group member having been stationary for 50%-68% of the observable time. The males did not exhibit sexual behaviors or interest in grooming the females while they were in swell. The group distributed nearly equal amounts of grooming to each male and both males spent nearly equal amounts of time in proximity to other members of the group. Mugsy, however, groomed others significantly more than Lu. Based on previous research, those that groom others more tend to be subordinate. The grooming data analyses determined the group's hierarchical structure to be Debbie < Kerry < Julie < Lu < Mugsy. The data also indicated that Lu is likely to be the next alpha individual when Debbie's status declines as she continues to age. Enclosure usage varied for the males and the females of the group. The patterns of enclosure usage replicated the natural fission-fusion social structure found in wild chimpanzees. The females were found to distribute the majority of their time near the waterfall/second viewing area and the males distributed their time near the first and second viewing area. Although the males and females were most often in separate groups, occasionally they were observed in one group moving through the enclosure or foraging and feeding together.

Overall, this captive group of chimpanzees did not demonstrate behavior characteristic of their sex and age. A variety of factors may have contributed to the observed behavior patterns, such as the lack of mixed-ages for each sex, lack of adult male role models, hand/peer-rearing of the adolescent males, and the presence of a strong female coalition; however, this study could not distinguish among these factors.

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CHAPTER I

INTRODUCTION

Evolutionary and environmental forces shape specific adaptive behaviors in animals that can be described as species-specific behaviors. When an animal is removed from its natural environment and placed in captivity, the animal experiences a variety of "unnatural" conditions that it would not encounter in the wild. Captive environments can create unnatural social groupings, are restricted and relatively predictable, are located in climates that differ from native climates, and may lack certain natural environmental stimuli that provide opportunities to express species-specific behavior. These deviations from the natural environment in which the animal has evolved can negatively impact an animal physically and psychologically. Burghardt (1996) suggested that captivity is controlled deprivation of many natural elements some of which are necessary for the expression of species-specific behavior at appropriate levels, and he encourages managers to view the animals and their captive environment holistically and understand how they interact. Managers need to have target behavioral benchmarks for captive animals based on their wild counterparts to evaluate what elements are needed for the expression of natural behaviors as well as for an animal's overall well-being (Burghardt, 1996). Therefore, investigations that provide insight into an animal's captive condition are valuable. In order to create conditions that contribute to the animal's well-being and mitigate the impact of captivity, management practices need to be based on the animal's life history, social and environmental requirements, and specific individual needs. Also, animal managers need to be able to identify elements or the lack of specific elements in an animal's environment that may be causing disruptions in normal behavior patterns.

Chimpanzees are an exceptionally charismatic species and share many characteristics with humans. As a result, chimpanzees have been popular animals to exhibit in captivity. They have proven to be a challenge to manage in captivity due to their complex intelligence, unique social structure, and aggressive tendencies. Studies of captive group dynamics and social organization can provide useful information for managers to make informed decisions with regard to current and future management practices.

The American Zoo and Aquarium Association's (AZA) Chimpanzee Species Survival Plan (SSP) manages the captive chimpanzee population in AZA institutions in order to maximize genetic heterogeneity and maintain demographic stability (American Zoo and Aquarium Association, 2005). While it focuses on the entire population it also must make decisions in the best interest of individuals. In addition, the management group is continually refining and defining the needs and requirements of captive chimpanzees based on new research developments. Since institutional transfers that result in the introduction of one or more individuals to an existing group of chimpanzees are common, managers need to have tools to assess and evaluate the group before and after an introduction.

Natural chimpanzee communities are comprised of multi-male/multi-female organization and intercommunity and intragroup aggression can occur (Goodall, 1986; Muller, 2002). Similar levels of aggression have been observed in captivity, such that it has become a major factor that managers must consider when introducing an unfamiliar individual to a new group, particularly males (Alford et al., 1995). The potential for injury and even death is very high during introductions. Regardless of the potential for

conflict, managers have realized that social housing is desirable to allow for an appropriate environment that can provide the necessary cues for normal physical and psychological health and development. Research has revealed that familiarization through visual and auditory contact before physical contact can reduce the levels of wounding aggression during introductions (Alford et al., 1995). In addition to the introduction methodology, research that elucidates an individual's behavior and/or the behavior of an existing group will also aid managers and the SSP to make appropriate decisions regarding the placement and introduction planning of particular animals. Captive chimpanzee group numbers and compositions vary around the globe and often require tailored management plans for the particular group. The Chimpanzee SSP is interested in establishing a database on the social interactions of specific group compositions. This database will aid them in determining the placement of animals and serve as a resource for other managers on how to best care for their group.

The social structure of chimpanzees often fluctuates between extremely dynamic and stable states. Social instability often occurs during the dynamic period where social ranks are not formalized or clear-cut. Primate social instability is characterized by frequent episodes of aggression and high rates of role reversals in dyadic relationships, where the stable state is characterized by low frequencies of aggression and ranks are relatively consistent and unchanging (Sapolsky, 1993). Knowledge of a group's stability or instability is valuable information for introduction timing and planning.

This investigation explored the social relationships of a unique group of five chimpanzees housed at the Knoxville Zoological Gardens, Knoxville, Tennessee. The main focus was on two adolescent males that had been peer-reared together as infants.

The social grouping is comprised of the two adolescent males, an older dominant female, and two mature younger females. The maturation of the two adolescent males will provide a unique opportunity to study dominance and social development. The lack of mixed ages for each sex results in an "unnatural" grouping for these individuals and allowed us to explore how this social grouping may affect specific social behaviors.

Chimpanzee Natural History

In the wild, chimpanzees live in multi-male/multi-female communities that range in size from 20 up to 100 individuals (Nishida, 1979). The community social structure has a rather fluid/loose social organization, where individuals form small temporary parties that disperse throughout the community's range, reunite with other members, then often disperse again into different parties (Boesch and Boesch-Acherman, 2000; Goodall, 1986; Ghiglieri, 1984; Nishida, 1979; Sugiyama, 1973; Sugiyama and Koman, 1979). This type of social structure is considered a fission-fusion social system. Boesch (1996) determined the mean relative party size for chimpanzees to be between 9 and 21% of the community, where variations in group size for the Taii chimpanzees was affected by general fruit availability, sexual opportunities, and hunting. Male members tend to be philopatric, remaining in their natal community and defending the community's range from neighboring males, where females tend to transfer between communities (Bygott, 1979; Goodall, 1986; Hayaki; 1988; Nishida, 1979; Pusey, 1978; Sugiyama, 1973)

As the philopatric sex, adult males form strongly bonded groups also known as "male clusters" and are considered the nucleus of the community (Fedigan, 1982; Pepper et al., 1999). The development of strong bonds between males serves to enhance their ability to work cooperatively when defending their territory (Bygott, 1979; Goodall,

1986; Nishida, 1979) and increases hunting success (Boesch and Boesch-Acherman, 2000). In order to protect a community territory, adult males need to work cooperatively, patrolling and defending the territory borders. Cooperative territorial defense by multiple males confers greater benefits than if each male individually defended a small territory and provides a larger feeding range, increased access to a larger number of females, and better ability to defend an area with lower risk to its party members (Bygott, 1979; Ghiglieri, 1984). Males will allow receptive (estrous) females to transfer between communities without attack (Bygott, 1979; Nishida, 1979). The females' conspicuous sexual swelling around their anogenital region becomes their passport between communities.

Adult males tend to exhibit a preference for associating with other adult males (Goodall, 1986; Hayaki, 1988; Nishida, 1979; Pepper et al., 1999). This observed preference could be considered a tactical decision and not a random or passive association (Newton-Fisher, 1999). Forming social bonds with other adult males creates the opportunity to develop alliances that will serve to increase an individual's social status (Bygott, 1979; Newton-Fisher, 1999), which in turn confers the benefits of greater access to resources such as estrous females and desirable foods (Leonard, 1979; Popp and Devore, 1979; Silk, 1987). Males appear to make strategic decisions as to which males make the best allies and then distribute their attention accordingly. Partner choice plays a crucial role in attaining social status. Social exchanges such as reciprocity and interchange are social strategies that wild chimpanzees have been reported to exhibit. These exchanges appear to serve the function of maintaining social bonds and achieving and maintaining high dominance rank (Watts, 2002). De Waal (1982) describes

chimpanzee behavior as political, where befriending high-status males can lead to increased tolerance and less competition for females and other valuable resources.

Females are less sociable than males and tend to spend most of their time with their offspring, except during times of estrous (Goodall, 1986). Once a female becomes sexually mature, she will travel independently and eventually begin a family of her own. Wrangham (1979) suggests that females disperse throughout the community range in order to maximize their feeding efficiency, which then contributes to her reproductive rate. When a female comes into estrous, she becomes more social and spends more time near the male members of the group. A female becomes more attractive to males during the stage of maximal sexual swelling and sexual behaviors increase (Shefferly and Fritz, 1992). At this time, the female becomes the center of attention in a male party (Goodall, 1986). Intermale agonism and tension increase when one or more estrous females are present (Shefferly and Fritz, 1992). When not in estrous, the female once again becomes more solitary.

Adolescent Males

When community males become independent from their mothers, they will join the adult "male cluster" and gain social rank within their natal community (Kawanaka, 1989; Nishida, 1979; Pusey, 1978). This process begins at early adolescence (6-12 yrs), when males begin to make the transition from a constant association with their mothers to social integration into the adult male group and begin to display sex-specific adult behavior (Pusey, 1978; Pusey, 1990). A fascination with adult males and strong interest in spending time in their proximity appears to be the primary factors motivating a young male to separate from his mother. Young males benefit from spending time in proximity

to the adult males by learning a variety of social skills such as effective charging displays and hunting skills that will enable them in the future to improve their status and reproductive success.

Adolescence is defined by characteristic physical, behavioral, and physiological changes. During this stage of development, chimpanzees experience a series of endocrinological changes that culminate in physical and sexual maturity (Pusey, 1990). During puberty, males experience a relatively rapid increase in testosterone levels, a growth spurt, and a dramatic increase in testicular size (Kramer et al., 1982; Nadler et al., 1987). Males in a stable, mixed sex social group, living in a semi-natural captive environment reached adult hormone levels by age seven and full dentition and growth by age nine (Kramer et al., 1982). These stages of development were defined as early adolescence at age seven and end of late adolescence at age nine, based on the corresponding physiological signals. In the wild, these stages are correlated with physical development at later ages. Pusey (1978) observed in the wild, the male growth spurt and increase in testicular size occur at 9-13 years of age, two years later than in captive chimpanzees. During the stage of late adolescence, reproductive maturity may be reached; however, behavioral and social maturity is not achieved until adulthood (Fedigan, 1982; Kramer et al., 1982).

In addition to physical and physiological changes, there is a notable developmental change in social behavior. Behavioral changes parallel physical changes, such as a decrease in play and an increase in autogrooming, hierarchical behavior, aggression, and sexual behavior (Kramer et al., 1982; Nadler et al., 1987). Adolescent males are strongly motivated to associate with adult males; however, young males are

subordinate to the adults and tend to be peripheral to the "male cluster" due to decreased tolerance and increased aggression towards them from the adult males (Hayaki and Huffman, 1989; Kawanaka, 1989; Pusey, 1978). Adolescent males groom adult males longer as they get older, although adult males rarely reciprocate grooming adolescents until they have approached full size (Pusey, 1978).

During this stage of social development, males are also attempting to improve their dominance status and begin to display, threaten, and attack females in an attempt to dominate them. By late adolescence most males consistently were dominant to females (Goodall, 1986; Pusey, 1978). This maturational phenomenon of dominance assertion during adolescence has been described as a biological imperative that becomes an important preoccupation for maturing males (Coe and Levin, 1980; Riss and Goodall, 1977). Among adolescent males the dominance relationships are not always apparent, because overt aggression towards another adolescent could elicit an attack by an adult male (Hayaki and Huffman, 1989).

Display behavior is an important aspect in achieving dominance. This form of agonistic behavior appears to develop through observational learning, where immature males watch, follow, and even imitate adult male display (Pusey, 1978). Acquisition of rank and carving out a position in the male social network begins by dominating females, followed by dominating senior and low ranking males then proceeds to those further up the rank (Bygott, 1979; Kawanaka, 1989; Nishida, 1979; Pusey, 1990). Integration into the adult male social group and attainment of high rank in the male hierarchy helps ensure a male's reproductive success, since males collectively patrol and defend the community range which encompasses multiple females (de Waal, 1982; Goodall, 1986;

Nishida, 1979) and contributes to the cooperation by females during copulation and consortship (Pusey, 1990). Through adolescence the form and frequency of aggression increases and continues to develop into a more adult form in wild chimpanzees (Pusey, 1990) as well as captive chimpanzees (Kramer et al., 1982).

Sexual behavior develops at a young age for males; however, typical adult pattern of courtship and copulation is not achieved until adolescence (Goodall, 1986). Copulation rates decline in adolescence due to inhibition by adult males (Pusey, 1990) and rejection by females (Pusey, 1978). The ability to dominate a female appears to be an important factor in cooperation during consorts and copulations.

Dominance Hierarchy

Dominance hierarchies have evolved as a result of a variety of environmental pressures in order to maximize survival and reproduction (Boesch and Boesch-Achermann, 2000; Goodall, 1986). Social dominance, generally speaking, is a fitness maximizing strategy and can be considered the consequence of self-interested actions based on the fact that dominant individuals traditionally have priority access to limited resources such as food and estrous females (Leonard, 1979; Popp and Devore, 1979; Silk, 1987). Dominant males can monopolize estrous females or mate-guard more effectively than those lower in rank (Cowlishaw and Dunbar, 1991; Goodall, 1986; Nishida,1979). Dominants have the ability to restrict the behavior of subordinates, while the dominant's behavior is not limited by the other (Chance, 1967; Deag, 1977). Rank and dominance are initially determined by aggressive encounters, observation of aggression, or result from community traditions (Goodall, 1986; Noe et al., 1980). Dominance among chimpanzees is established and maintained through aggression and displays as well as

keeping close association with top ranking males (Nishida, 1979). High ranking males direct the greatest amount of aggression towards a large percentage of other individuals, seldom receive threats or attacks, and receive a high percentage of submissive gestures from others (Riss and Goodall, 1977). Rank, however, is not always fixed and role reversals are not uncommon. Social rank can change over time with the formation of alliances and coalitions, such that with the support of one or more individuals, a subordinate can gain status or simply win in an aggressive encounter with a higher-ranking individual (de Waal, 1982; Riss and Goodall, 1977). Chimpanzee males tend to show a relatively clear-cut hierarchy, whereas the females' hierarchy tends to be more ambiguous (Nishida, 1979; Riss and Goodall, 1977). Understanding a dominance hierarchy in a social system allows one to make predictable assumptions with regard to relationships and outcomes of certain encounters. Dominance is not just a structure, but a process (Leonard, 1979). Males often make strategic decisions with regard to behavior and with whom they associate. Strategic and tactical decision-making can be considered fitness-maximizing behavior which then directly relates to dominance position (Deag, 1977; Leonard, 1979). Dominance is challenged under a number of circumstances, such as when parties reunite, when there is a limited desirable resource, when status relations are unclear, and when a maturing group member is striving to improve his rank (Bygott, 1979; Coe and Levin, 1980). Bygott (1979) found that 90% of all agonistic interactions involved at least one male.

Dominance rank may be clear-cut but is not necessarily a rigid structure. De Waal (1982) suggests that there are two layers to the social organization, a stable formal layer of dominance and a flexible layer of real dominance. The stable formal layer of

dominance is the clear-cut rank indicated by direction of ritualized signals, where the flexible layer of real dominance is when a subordinate, under certain circumstances, can either win an aggressive encounter or have priority access to a resource (de Waal, 1982; de Waal, 1986). For example, a female may gain a temporary higher social position after giving birth or during estrous, but essentially her formal position remains the same (Noe et al., 1980). Social tolerance is another aspect that affects the prediction that a dominant individual will have sole access to a resource. A dominant individual expresses social tolerance by suppressing his position and allowing a subordinate individual access to a resource. Food sharing and allowing access to estrous females are examples of social tolerance, such that the dominant individual is controlling the resource without taking priority (de Waal, 1982; de Waal, 1986; Noe et al., 1980; Vervaecke et al., 1999).

Dominance has also been explored with respect to social bonding. De Waal (1986) explored this relationship to help develop an understanding of intragroup aggression and the social cohesiveness of chimpanzee groups. He asserted that dominance hierarchies help maintain a cohesive network of social bonding and mutual dependencies. Dominance hierarchies are maintained by formalized unmistakable signals and when conflict arises the winner offers conditional reconciliation and social tolerance if the loser assumes the subordinate position. These mechanisms create cohesion and stability and seem to reduce levels of aggression. Dominance hierarchies are maintained by both the subordinate and the dominant individual's behaviors (Deag, 1977). Coe and Levin's (1980) research has also illustrated that chimpanzee dominance is most often expressed through ritualized signals and non-contact dominance behavior rather than overt aggression. Chimpanzees have a large repertoire of aggressive/submissive

ritualized signals that minimize the potential for conflict and injury. Cooper (1990) found that high-ranking animals received the most grooming and greetings. These behaviors seemed to help maintain social organization, leading to less frequent aggressive interactions and conflict.

There are several measures used for determining dominance. An overall picture of the dominance structure can be determined by the direction in which aggressive and submissive behaviors occur, such as approach-retreats, pant-grunts, presenting, and the expression of agonistic behaviors (Goodall, 1986; Zumpe and Michael, 1986). Pant-grunting is performed unidirectionally for males, with those of lower status performing pant-grunts to those of higher rank (Bygott, 1979; Noe et al., 1980). Approach-retreats are characterized by the lower ranking individual moving out of the way of the dominant. Status is often determined by the outcome of an aggressive/agonistic encounter where there is a district winner and loser. Another pattern of submission is presenting or turning of the rump towards the dominant animal (Goodall, 1986). When a limited resource is available, those of higher social status will have greater access to the resource. Dominant individuals also receive a higher proportion of attention from other members (Cooper, 1990). A dominant individual is often located in a focal position near the group's spatial center, where subordinates tend to orient their behavior in relation to the dominant (Chance, 1967).

Grooming

Social grooming is a commonly observed activity among many primate societies. Grooming serves the utilitarian function of ectoparasite removal and skin cleansing (Hutchins and Barash, 1976), functions in strengthening social bonds (Dunbar, 1991;

Watt, 2000), and can be exchanged as a commodity for reciprocal grooming or interchanged for other services (Barrett et al., 1999; Hemelrijk and Ek, 1991; Vervaecke et al., 2000; Watt, 2000). In addition, grooming can also serve as a tension reducing mechanism (Goodall, 1986; Terry, 1970) and can be utilized during reconciliation and consolation between individuals (de Waal and van Roosmalen, 1979).

Research has revealed that grooming sessions are not random or equally distributed among individuals of a population. Grooming is a social bonding activity, such that grooming an individual will help strengthen bonds and create familiarity. High-ranking individuals are more attractive as a partner because they can offer effective support during agonistic encounters and share valuable resources (Seyfarth, 1980). Therefore, individuals are adapting their behavior to maximize personal benefit. For males and females, high-rank has been positively correlated with significantly more grooming than lower-ranking individuals (Goodall, 1986; Hemelrijk and Ek, 1991; Nishida, 1979; Seyfarth, 1977; Seyfarth, 1980; Simpson, 1973; Watt, 2000). Schino (2001) performed a meta-analysis of grooming behavior of 14 species of female monkeys and determined that social rank correlated with grooming received and that females competed for access to high-ranking females as grooming partners. Vervaecke et al. (2000) also found that bonobos (*Pan paniscus*), a close relative of the chimpanzee (*Pan troglodytes*), exchanged grooming for support and that grooming was distributed according to rank. Alliance formation and support in agonistic encounters have been associated with the degree of attraction between individuals and the strength of interindividual bonds (Hemelrijk and Ek, 1991; Watt, 2000).

Nishida (1979) found that 46% of the total grooming occurred between adult males, 39% between males and females, and only 10% among females. Females on average tend to be more individualistic, where males are very sociable and gregarious. Female sociability, dominance rank, and grooming interactions with males increase during times of estrous; however, this is temporary and their behavior changes as their physiological condition changes (Nishida, 1979). Affiliative relationships between males and cycling females, predominantly involve high-ranking males (Matsumoto-Oda, 2002).

Captive Rearing Conditions and Social Group Composition

Rearing condition and social group composition are two very important factors that have been identified as critical components to the development of a healthy, socially capable individual. Unfortunately, the ideal captive conditions where a mother always rears her offspring and a social group comprised of a mixed-age and mixed-sex in a semi-natural captive environment is not always possible. With respect to rearing, chimpanzee mothers do not always express appropriate maternal care; thus, human rearing becomes a necessity for the infant's survival. The decision to human-rear an infant chimpanzee is always a difficult one and is usually the last resort. Research has revealed that rearing conditions play an important role in the development or lack of development of appropriate sexual behavior, age-specific behavior, and species-specific behaviors. Behavioral development of juvenile and adolescent chimpanzees tends to resemble their wild counterparts when born in a complex breeding group and remain there until sexually mature (Bloodsmith et al., 1994). Infants reared in restricted environments display few species-typical behaviors, avoid contact, play less, copulate infrequently and exhibit aberrant behavior (Turner et al., 1969). As social deprivation increases there are

reduced levels of normal behavior and an increase in the display of abnormal behaviors (Martin, 2002; Sackett, 1967).

Replicating the stimulation and social environment that a mother and naturalistic social group provide is difficult in a hand-rearing unit. However, it has become a priority to attempt to replicate it as closely as possible in order to shape a psychologically and physically healthy, socially competent, sexually functioning individual. Peer-rearing has become a preferred option as opposed to hand-rearing an infant separately. Fritz and Fritz (1985) found that peers provide some of the necessary stimulation that can mitigate the effects of maternal separation and provide the hand-reared infants with the opportunity to develop a social relationship with a conspecific as opposed to exclusive bond formation with the human caregiver. Social competence is essential for a successful integration into a social group; therefore, early appropriate social relationships helps an infant develop the necessary skills to build relationships with conspecifics in the future. Chimpanzees raised in peer groups show similar levels of interactivity and social play as those raised in semi-natural zoo settings indicating similar social development (Spijkerman et al., 1996). For peer-reared individuals, peers can also serve as primary attachment figures aiding in the alleviation of stress and serving as a source of security (Higley et al., 1992).

Research on social and sexual competence in peer-reared individuals has had variable results. The age at which an individual is peer-reared appears to be an important factor. Turner et al. (1969) found that animals isolated from birth to age three displayed emotional disturbances, reduced interest in other animals, were sexually inept, and had impaired learning. Six to nine years after isolation, the animals progressed towards

normal species-typical behavior; however, continued to do demonstrate deviant behaviors. Spijkerman et al. (1997) found that the lack of opportunity for observational learning had no measurable effect on the development of sexual behavior and amount of grooming among peers in peer-reared adolescent when compared to a family group. Spijkerman et al.'s (1997) also showed that peer-reared chimpanzees did not differ from the zoo family group with regard to conflict, support, and reconciliation. These results imply that peer-rearing aids in the development of appropriate social interactions. The adolescents of this study were peer-reared at 2 months of age or they were late separated from their mothers at 12 months then were peer-reared. Fritz and Fritz (1985) research on hand-reared and peer-reared animals has led them to believe that the rearing environment during the first year of life is critical for the development of appropriate socio-sexual behavior.

Human-reared chimpanzees often develop stereotypical behaviors. Rocking behavior is a commonly observed stereotypy in human-reared chimpanzees and is thought to be a form of self-stimulation to replace the stimulation normally provided by the mother. Fritz and Fritz (1985) believe that rocking behavior is an indicator of a disturbed maturational process, and those that exhibit rocking tend to exhibit social and motor problems later in life. They also found that rockers are never dominant or successful breeders.

Other studies on primates with similar dominance hierarchy social systems and multi-male/multi-female groupings, illustrate that early experience can be a useful predictor of future social success. For example, mother-reared Rhesus Macaque monkeys were dominant to peer-reared individuals (Bastian et al., 2002). Anderson and

Mason (1974; 1978) found that higher-order social skills are dependent on social rearing conditions, where socially experienced animals appeared to be able to take into account more social information and behave accordingly.

Knoxville Zoo Chimpanzees

The Knoxville Zoo's group of chimpanzees is unique with regard to its social organization and composition. First of all, the dominant individual is a mature female approaching old age; there are two younger mature females (one being the dominant's daughter), and two peer-reared adolescent males. The two younger mature females are not sexually experienced nor are the adolescent males. The males have never lived with an adult male, which has limited their ability to observe normal adult male behavior. Since the males have been the youngest members of the group, all females have been dominant over them and the females have also been known to form coalitions against the males during agonistic interactions. In 2001, the keepers noticed an increase in the frequency of agonistic interactions as the two males entered adolescence. The keepers were interested in understanding the group's social dynamics and were curious as to whether the males were beginning to challenge the females and which male would be the next alpha individual.

The adolescent males have a unique history. In 1991, Mugsy and Lu were transferred to the Knoxville Zoological Gardens (KZG) as infants to be peer-reared and integrated into the existing group of chimpanzees. The existing group was a mixed-age maternal group consisting of two mother/daughter dyads. The first full contact introduction resulted in an aggressive attack by an adult female, injuring both infants. A

more systematic approach was implemented in April 1993 and by July 1994 a successful assimilation was achieved (Drummer, 1995).

At the beginning of the study, Mugsy and Lu were 11 years old and in the stage of early adolescence. The keepers' informal observations corresponded with the expected behavioral changes that adolescent male chimpanzees experience at this age, such as increased levels of agonistic behavior and attempts at dominating the females of the group. It was suspected that interesting social dynamics would be observed at this point in their lives and their future status in the group will depend on their interactions with the other members.

Debbie, approximately 30 years old, has been the oldest and observed dominant member of the group for the past several years since the previous alpha female died. With the observed increase in aggression, the keepers noted that during episodes of aggression it appeared that it was males versus females. However, keeper observations have indicated that Lu is the most aggressive as well as the preferred male, indicating that he may be the leading candidate for the dominant position in the group. The assumed dominance hierarchy is Debbie > Kerry > Julie > Lu > Mugsy, based on personal communications with the Great Apes Department at KZG.

No detailed studies have been performed on the group for social structure since the males entered adolescence. This research attempted to determine how the group's hierarchy was structured and whether the males were exhibiting characteristic behaviors of healthy, socially capable, adolescent male chimpanzees. An important aspect of this research was to understand how this group composition and particular unique social backgrounds have affected the expression of "normal" behavior patterns. Based on

previous research, the males should have been attempting to dominate the females and raise their status within the group. The males were expected to perform agonistic displays and aggression towards the females and to each, as well as sexual behaviors towards the females. An analysis of aggressive, submissive, sexual, proximity, and grooming behavior should reveal the social hierarchy and which male will be the next dominant member of the group. This study also investigated the overall behavior of each group member while on-exhibit.

CHAPTER II

METHODS

Subjects

The subjects, five captive chimpanzees (*Pan troglodytes*) housed at the Knoxville Zoological Gardens (KZG), Knoxville, TN, consisted of three adult females and two adolescent males. The group composition has been stable and constant since Mugsy and Lu were socially integrated as infants in 1994. Table 1 illustrates each chimpanzee's history.

Primarily, the group's main diet was provisioned while off-exhibit. They received their main diet before they left their night quarters and when brought in for the evening from the outdoor exhibit. Around noon, fruits, vegetables, and other various

Table 1. Chimpanzee subjects at the Knoxville Zoo.

Name	Sex	Date of Birth	Acquisition	Origin	Age at onset of study	Age at end of study
Debbie	**F**	**~ 02 /1971**	**1976**	**Pet**	**30**	**32**
Kerry	**F**	**03/19/88**	**----------**	**Knoxville Zoo**	**13**	**15**
Julie	**F**	**03/28/86**	**----------**	**Knoxville Zoo**	**15**	**17**
Lu	**M**	**11/24/90**	**05/16/91**	**Lowery Park Zoo**	**11**	**13**
Mugsy	**M**	**06/21/90**	**05/16/91**	**Los Angeles Zoo**	**11**	**13**

edible enrichment items were provided while on-exhibit. The noon food and enrichment items were thrown to each group member individually to minimize competition.

Females

Debbie, the oldest dominant member of the group, was 30 years old at the on set of the study and considered a mature female approaching old age. Before her arrival at KZG, she was privately owned as a pet and in 1976, at five years of age, she was donated to KZG. Debbie assumed the dominant position in 1995 when the previous dominant female died. Kerry is Debbie's only offspring and was born at KZG in 1988. Debbie and Kerry have maintained an exceptionally close bond over the years. Julie was born in 1986 and mother-reared at KZG by a female that is now deceased. At the beginning of the study, Julie was 15 years old (mature) and Kerry was 13 years old (adolescent). Julie was considered sexually mature at the beginning of the study, where Kerry entered into sexual maturity across the course of the study. Neither has reproduced or been with a sexually experienced male per the decision of the Chimpanzee SSP. All females were on a form of contraception. Kerry was contracepted with a norplant implant and Julie and Debbie were administered birth control pills.

Males

The two males of the group, Mugsy and Lu, entered the age class of late adolescence during the study period. Lu experienced a growth spurt around 1999, where Mugsy's occurred around 2001 (Figure 1). Their growth spurts are indicative of puberty, when the males become physically and sexually mature. Both Mugsy and Lu shared a similar rearing background. As a result of inadequate maternal care, both males were

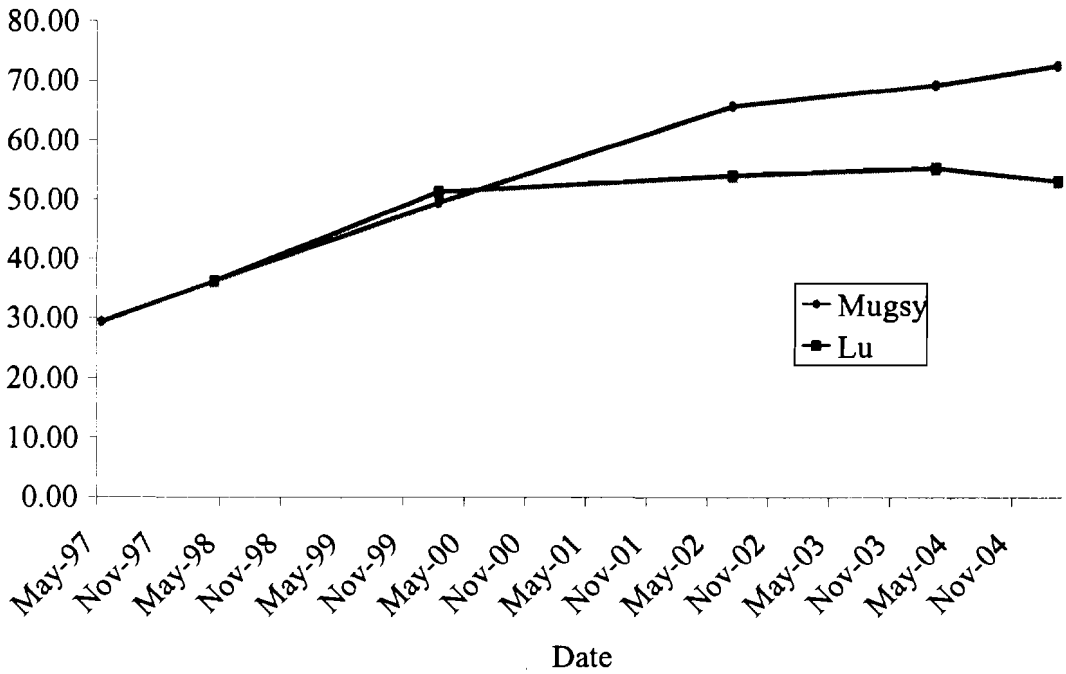

Figure 1. Mugsy and Lu's weight in kilograms over time.

removed from their mothers at infancy and were human-reared at their respective zoos. Mugsy was born in June 1990 at the Los Angeles Zoo in California. For the first year of his life he was socially isolated from other conspecifics. He was transferred to KZG in May of 1991 to be peer-reared with Lu, a similar aged infant. During his first year of life Mugsy developed stereotypic rocking and scooting behaviors that have persisted over time but with lessened frequency. These behaviors are common in hand-reared chimpanzees and appear to be a coping mechanism to deal with maternal loss and restricted rearing (Martin, 2002). Lu, born November 1990 at Lowery Park Zoo in Florida was transferred to KZG at six months of age to be peer-reared with Mugsy. Lu did not develop the same stereotypic behaviors as Mugsy; however, he has exhibited a strong attachment to some of his human caregivers at KZG.

Enclosures

Outdoors

Behavioral observations were conducted at the outdoor exhibit area (Figure 2), which consisted of an extensive naturalistic setting, including a waterfall with a small pool at the base, live trees and snags, rock structures, a man-made termite mound, vines, and grass. The total exhibit area was approximately 5058m^2, with two public viewing areas, both of which were utilized for the observations reported below.

Indoors

Adjacent to the outdoor exhibit was an indoor courtyard where observations were also conducted (Figure 3). The group was given access to this area during inclement weather or when the outdoor exhibit was under construction. The courtyard was approximately 10.5m x 10m with a mesh top and glass viewing area. Metal bars separate the courtyard and outdoor exhibit. Contained within the courtyard were ropes, wood wool, wooden poles for climbing and sitting, a wooden platform, plastic barrels attached to the ceiling, and a woven hanging bed. Their night quarters were attached to the courtyard.

Dependent Variables

The dependent variables were specific target behaviors and exhibit locations. An ethogram was utilized for the study, which is a comprehensive list of potential behaviors that may be observed during an observation session (Appendix A). The ethogram, listing the behaviors, codes, and functional and topographical descriptions of each behavior, was derived from Drummer's (1995) social integration study with Lu and Mugsy when they were infants.

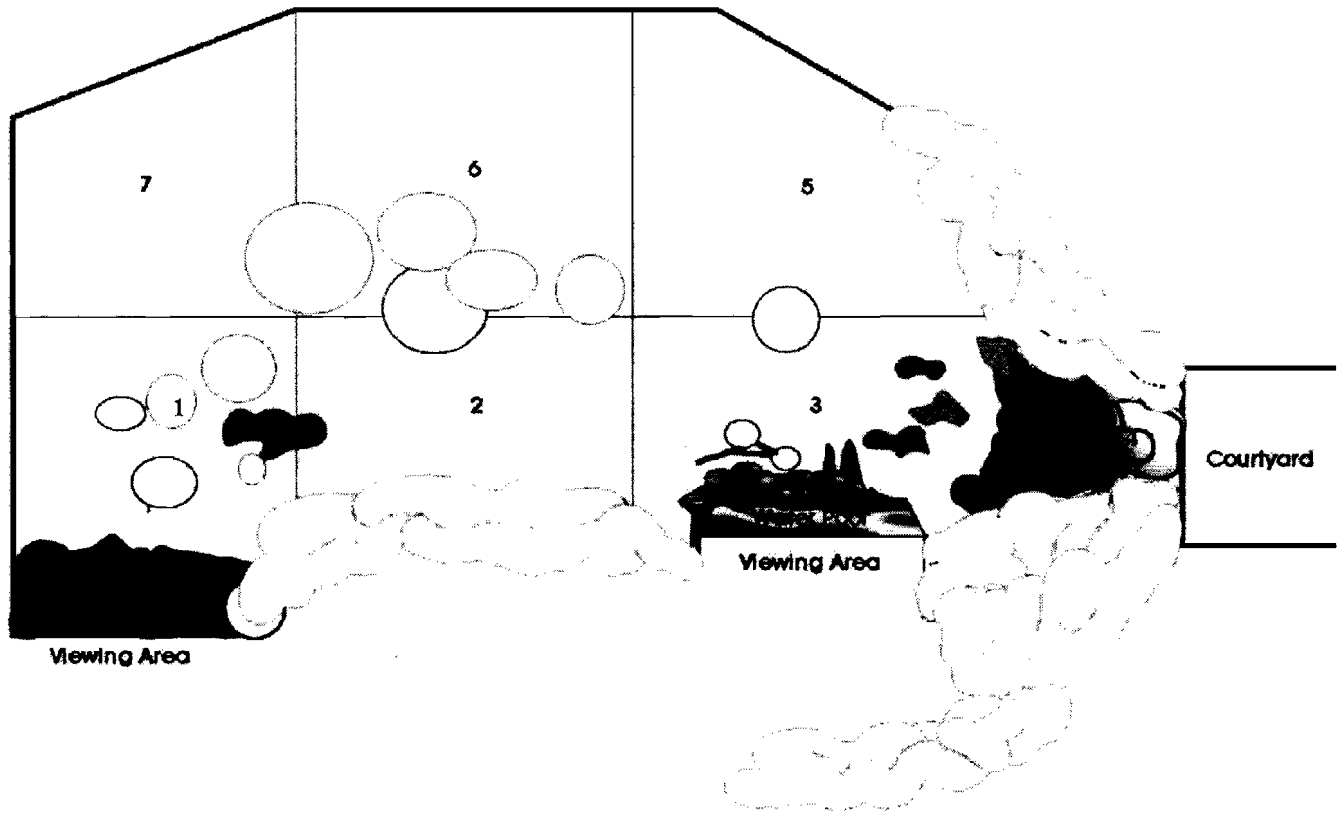

Figure 2. Outdoor exhibit area. Lines and numbers represent arbitrary delineation of the exhibit to determine area usage.

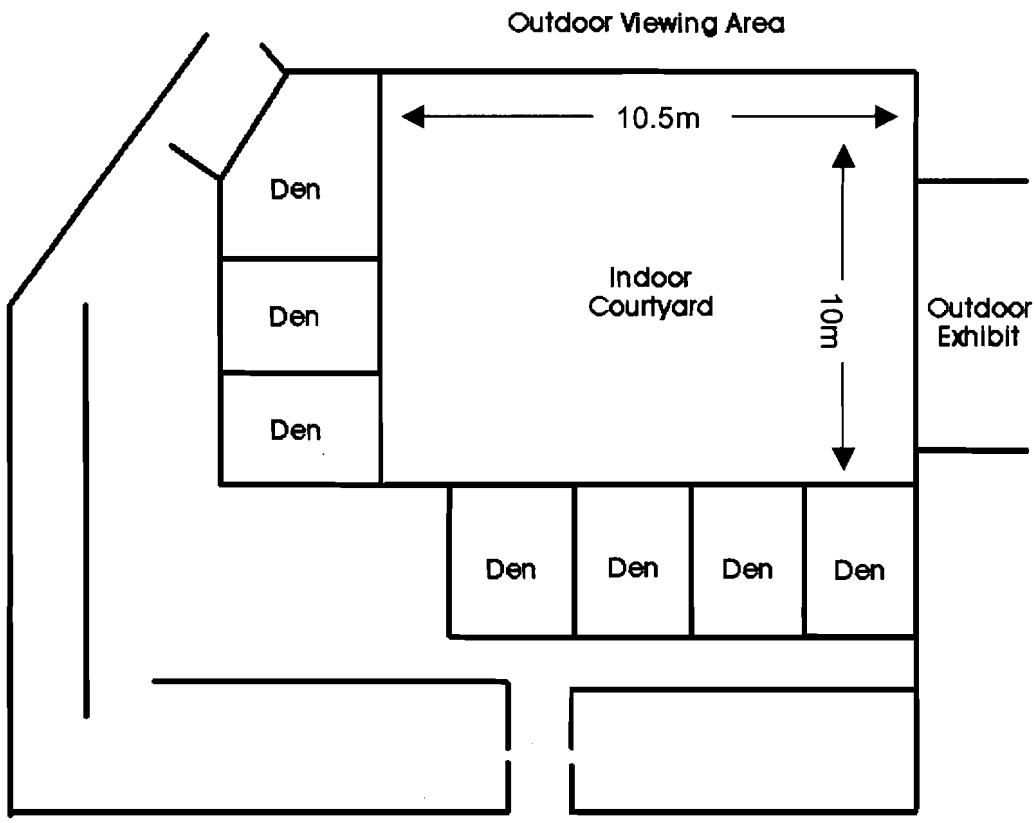

Figure 3. Indoor courtyard with night quarters. Figure from Drummer (1995).

Procedure

Behavioral data were collected using momentary time sampling of focal animals, which provided for measures of duration and frequency for specific target behaviors (Saudargas and Lentz 1986). The sampling interval occurred every 15 seconds, in which any target state behavior occurring at that time was coded on an observation form (Appendix B). Target event behaviors were continuously recorded as they occurred. Each focal animal was observed for a 20-minute time period. Observational data were collected between October 2001 and June 2003 between the hours of 1000 and 1600. This time frame was chosen due to zoo hours and group access to the on-exhibit areas. A total of 150 hours were used for data analysis. Observation sessions were conducted approximately 2-3 days per week. Approximately an equal number of observation sessions were recorded for each member of the group. In order to obtain an equal sample for all members of the group, a rotation procedure was used, where one individual was observed for a 20-minute session followed by an observation session on a different individual. Observation sessions were cancelled when the separation of a group member limited access and social interaction or when cold weather prevented the group from being exhibited. When on-exhibit, depending on the group's location, observations were taken from one of the two on-exhibit viewing areas or the courtyard viewing area. Focal animal location and movement were documented throughout the exhibit area.

Interobserver Reliability

Eight observers were trained to code the target behaviors and location. Interobserver reliability was performed among the data collectors. Twenty-four tests of reliability were performed and reliability ranged from 33% (anogenital inspection) - 100% (rock). Overall reliability across all behavioral categories was 82% (agree/agree + disagree). Reliability for certain behaviors was lower due to observer perspective and the angle in which the animal was facing.

Data Analysis

The focal animal sampling behavioral data were summarized to obtain frequency and durations of target behaviors. To explore individual differences, a descriptive analysis of the mean percentages for state behaviors were calculated and represented by a histogram to illustrate each individual's overall activity pattern. Specific target behaviors, such as grooming, displays, agonistic behavior, and presenting, were analyzed to determining the direction of interactions between individuals. Proximity was also assessed to examine the amount of time group members spent within one meter of the focal male.

Grooming and proximity data were determined over all the observation sessions for an analysis of which male received more grooming, groomed others more, and spent the greatest amount of time in proximity to others. Nonparametric techniques were used due to the non-normal distribution of data and the lack of homogeneity of variance. The Mann-Whitney U rank-order test for independent samples was employed to reveal if one male's percentage for grooming and proximity had a greater number or ranks than the other (Davis and Smith, 2005). All tests were two-tailed, and an alpha level of 0.05 was

chosen to determine significance. The Mann-Whitney U was performed on the males' grooming relationship data with all other members of the group as a whole, with females only, and finally with each individual. The same procedure was performed on their proximity data.

In addition, the number of days grooming occurred during the time the females were in swell and non-swell was calculated and analyzed using chi-square. This analysis explored the relationship of grooming interest and the females' reproductive condition.

Descriptive analyses and histograms were used to determine enclosure usage by exploring the percentage of time each chimpanzee spent in a particular area of the outdoor exhibit.

CHAPTER III

RESULTS

Overall Behavior Analysis of Focal Individuals

Each chimpanzee's overall activity pattern was analyzed to determine how they spent their time while on-exhibit. See Appendix A for descriptions of state behaviors utilized for the analyses. The mean percentage of time spent in each state behavior that was greater than 1% of each chimpanzee's observable time is represented in Figure 4. For a summary table of percentages, see Appendix C, Table A1.

Lu

Lu spent the majority of his time remaining stationary. He was stationary for 67.98% of visible time, which was more than any other group member. He spent 11.72% of his time engaging in the category of other behaviors, traveled 9.06%, and performed object manipulation 4.02% of the time. He groomed others and himself 4.12% and was groomed by others 4.07% of the time. Lu was observed watching other group members or the public 2.35% of the time. All other state behavior categories were observed less than 1% of the time (follow, agonistic, display, frustration/tantrum, social play, rock, fear, anogenital inspection, mount/thrust, closed-grin, and open-grin).

Mugsy

Mugsy was stationary 57.65% of the time and traveled 14.13% of the time. Mugsy spent more time traveling than any other group member. He spent 11.96% of the time grooming himself and others and was groomed by others 3.69%. He exhibited other

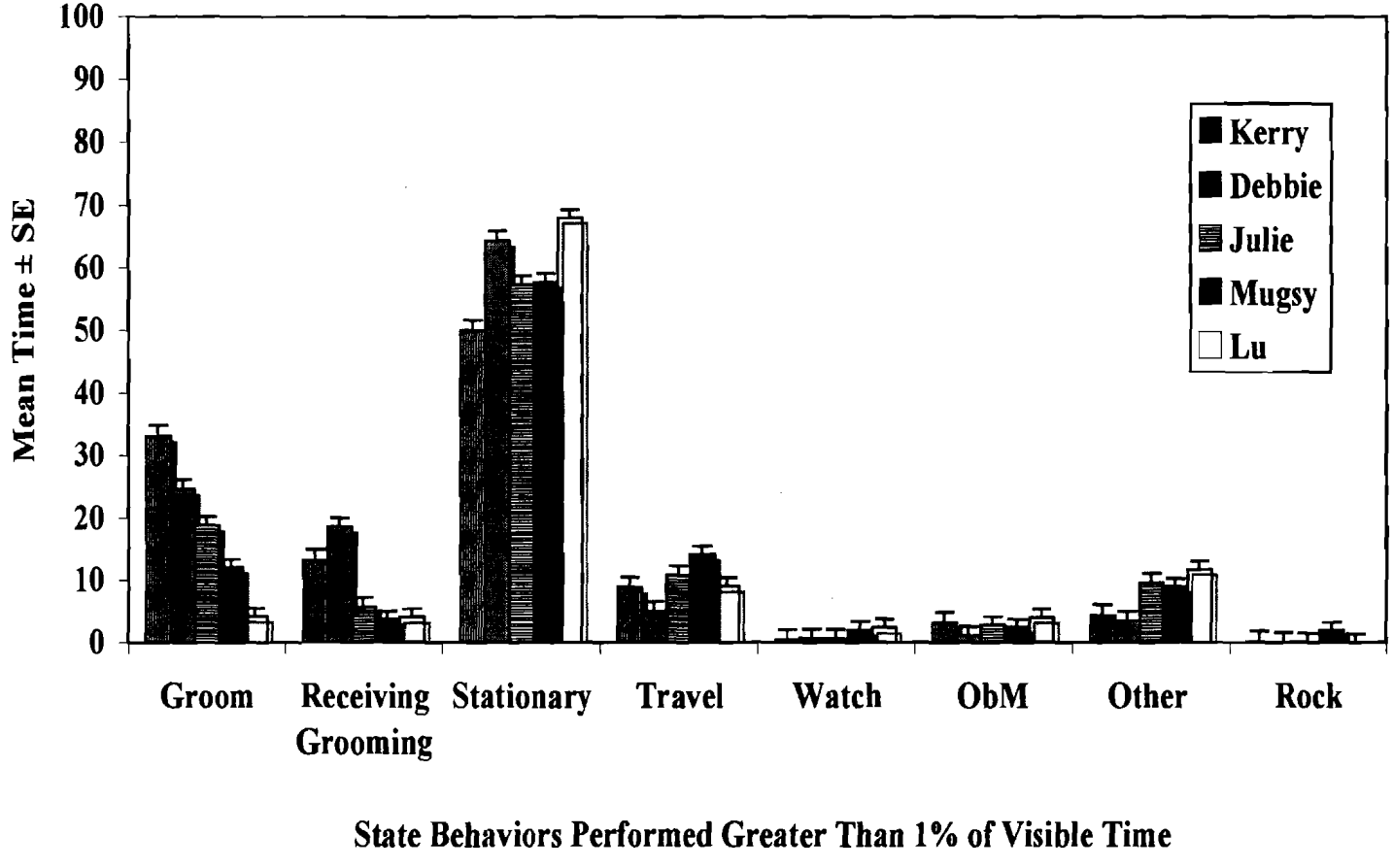

Figure 4. Mean percent time (±SE) each focal chimpanzee spent in general state behaviors for greater than 1% of the visible time.

behaviors 8.86% of the time. Object manipulation was performed 2.36% of the time and he watched other members of the group and the public 1.92% of the time. He rocked 1.9% of the time, which only occurred when he was in the courtyard with no access to the outside exhibit. Other state behavior categories were observed less than 1% of the time (follow, agonistic, display, frustration/tantrum, social play, fear, anogenital inspection, mount/thrust, closed-grin, and open-grin).

Debbie

Debbie was stationary 64.24% of visible time. She groomed others and herself 24.63% and received grooming 18.49% of the time. Debbie received the greatest percentage of grooming compared to the other members. Traveling was observed 4.99% of the time, which was the least amount of travel out of the group and could be attributed to her age. She engaged in other behaviors 3.50% of the time. All other state behavior categories were observed less than 1% of the time (follow, agonistic, display, watch, frustration/tantrum, social play, rock, fear, anogenital inspection, mount/thrust, closed-grin, and open-grin).

Kerry

Kerry was observed stationary 49.88% of the time. She groomed herself and others 33.05% and was groomed 13.22% of the time. Kerry had the greatest amount of time spent grooming herself and others. She traveled 8.8%, manipulated objects 3.14%, and performed other behaviors 4.33% and of the time. All other behaviors were observed less than 1% of the time (watch, follow, agonistic, display, frustration/tantrum, social play, rock, fear, anogenital inspection, mount/thrust, closed-grin, and open-grin).

Julie

Julie was stationary 57.27% of the time. She groomed herself and others 18.75% and was groomed 5.74%. She traveled 10.72%, performed other behaviors 9.56%, and was observed manipulating objects 2.67% of the time. All other behaviors were observed less than 1% of the time (watch, follow, agonistic, display, frustration/tantrum, social play, rock, fear, anogenital inspection, mount/thrust, closed-grin, and open-grin).

Male Adolescent and Dominance Behavior

Mugsy and Lu did not demonstrate behaviors characteristic of adolescent male chimpanzees. Agonistic and sexual behaviors were not observed and displays were observed less than 1% of the time for each male. The adolescent males did not form their own male cluster either. Mugsy was more proximal to Lu more often than he was proximal to the females, and Lu nearly equally distributed his time with Mugsy, Kerry and Debbie (Table 2). Mugsy spent more time grooming Lu than vice versa (Table 3). Overall grooming percentages were low except for self-grooming.

Table 2. Mean percent time each chimpanzee was proximal to other members.

	Lu	Mugsy	Kerry	Debbie
Lu				
Mugsy	**5.03**			
Kerry	**4.18**	**2.43**		
Debbie	**4.56**	**3.03**	**24.77**	
Julie	**3.00**	**2.42**	**18.53**	**13.95**

Table 3. Mean percent time each chimpanzee spent grooming themselves and other members of the group.

	Groomer				
	Males		Females		
Receiver	**Lu**	**Mugsy**	**Debbie**	**Kerry**	**Julie**
Lu	3.48	2.42	2.89	0.03	0.21
Mugsy	0.30	5.13	2.35	0.32	0.27
Debbie	0.87	2.56	5.26	17.04	6.67
Kerry	0.07	0.01	9.70	6.12	2.25
Julie	0.00	0.33	4.12	2.87	8.79

Exploring Grooming

Grooming data were combined for each member of the group from all observation sessions to obtain the total time spent grooming others and receiving grooming (Table 3). See Appendix C, Figure A1 for a histogram of the grooming data. The data revealed that Debbie was the preferred grooming partner for the other members of the group, followed by Kerry, Julie, Lu, and then Mugsy. All members of the group exhibited higher levels of self-groom than grooming other group member, except for Kerry and Debbie who groomed each other more than they groomed themselves or others. The females tended to spend more time grooming and distributed a greater percentage of their grooming to each other than the males. However, Debbie did distribute some grooming to the males, where Kerry and Julie groomed the males less than 1% of the time. Lu groomed himself the most and all other group members were groomed less than 1% of the time. Mugsy

spent more time grooming than Lu. Mugsy groomed himself the most, then distributed nearly equal amounts of grooming to Debbie and Lu, where Kerry and Julie were groomed less than 1% of the time.

Comparing Grooming and Proximity Data for the Males

The Mann-Whitney U was utilized to determine if a significant difference existed between the males with regard to the amount of grooming given and received and the amount of time other members of the group spent in proximity to each male. This analysis helped reveal which male was more dominant based on if he received more grooming than he gave and if one male was more proximal to other members of the group indicating a higher degree of sociality. See Appendix C, Table A2-A4 for tables of means for percent time and the p-values.

Comparing Grooming

Figure 5 illustrates the amount of grooming each male received by other members of the group as a whole, by females only, then grooming by individual. Lu received more grooming from all group members as a whole, yet not significantly more. The females as a group groomed Lu more than Mugsy, but this difference was also not significant. A further breakdown of the group members revealed Mugsy received more grooming than Lu from Julie and Kerry, but not significantly more. Lu received more grooming than Mugsy from Debbie, which was not significant. Lu received more grooming from Mugsy than Mugsy from Lu, but this difference was not significant. Overall, there was no significant difference between the males in grooming received from other members of the group, indicating no grooming preference for one male.

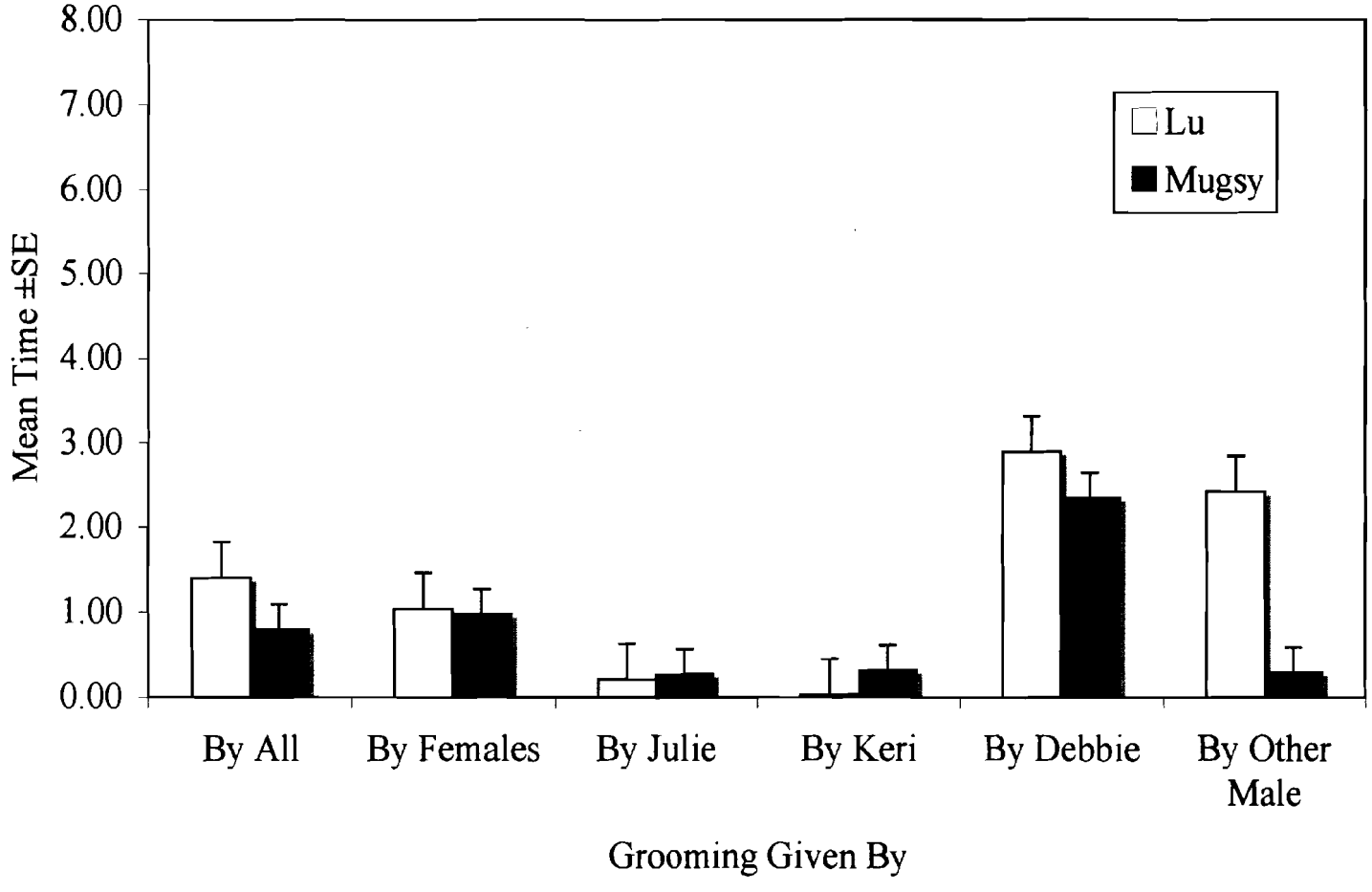

Figure 5. Mean percent time (±SE) grooming was given to each male by other members of the group.

Figure 6 illustrates the amount of grooming given to other members of the group as whole, females only and to each member by the males. Mugsy significantly groomed all other members of the group as a whole and the females only more than Lu. Mugsy significantly groomed himself, Julie, and Debbie more than Lu. Lu groomed Kerry more than Mugsy but the difference was not significant. Mugsy groomed Lu more than Lu groomed Mugsy, however, not significantly more.

Comparing Proximity

The data revealed that Lu was closer to all members of the group as a whole, to the females only, and closer to each individual female than Mugsy (Figure 7). However, none of these differences were significant. This indicated that both males were nearly equal in their sociability with other group members.

Grooming and Female Reproductive Condition

Table 4 illustrates the number of days a grooming session occurred during each female's swell and non-swell sexual cycle. Male chimpanzees of all ages are attracted to females with sexual swellings. The swelling around their anogenital region indicates that the females are in estrous. A chi-square analysis was performed on the data to determine if the males were more interested in a grooming relationship during a particular phase of their reproductive cycle. The analysis revealed that neither male showed a significant interest during swell or non-swell for Debbie (df=1, $x^2 = 0.0291$), Julie (df=1, $x^2 = 0.0001$), or Kerry (df=1, $x^2 = 0$).

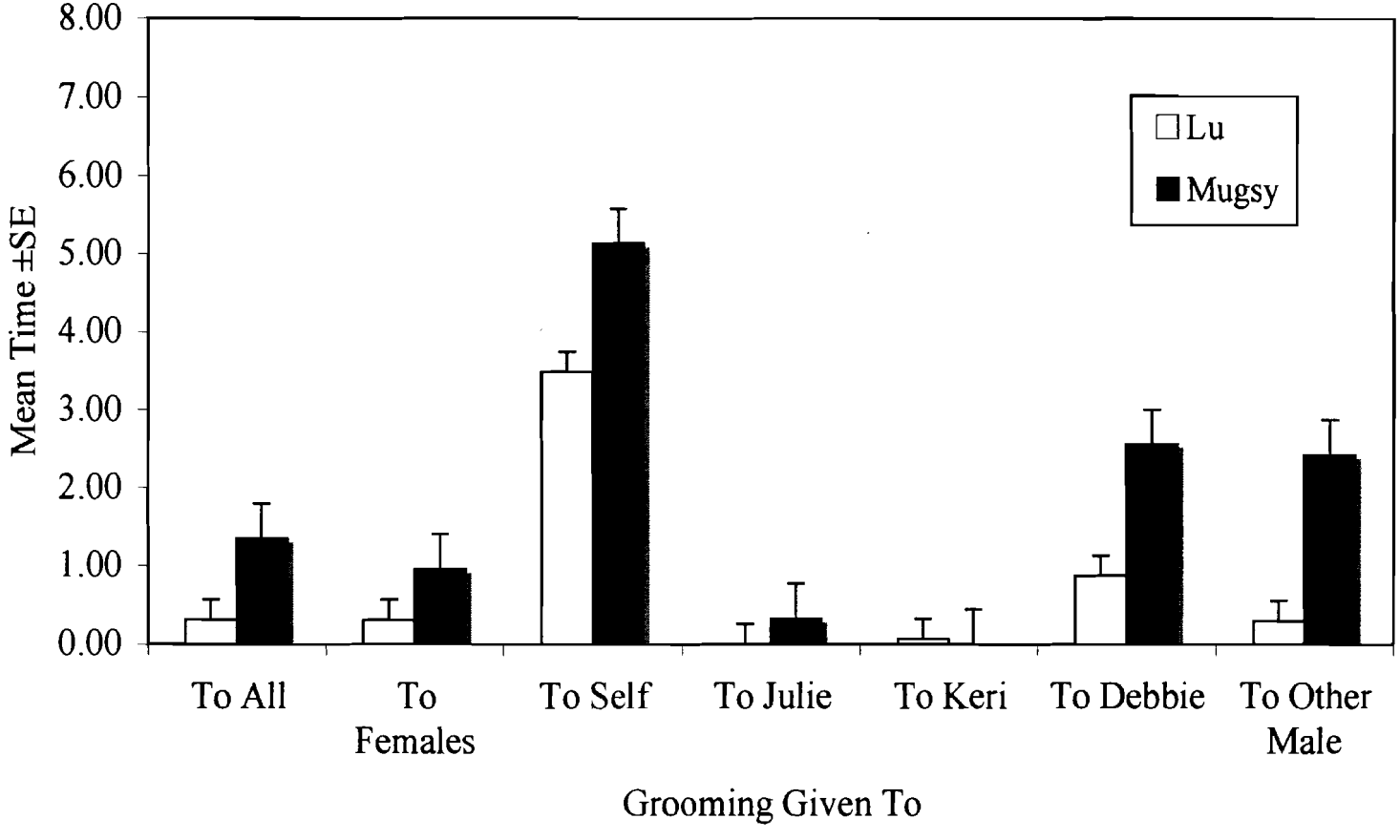

Figure 6. Mean percent time (±SE) grooming was given to other members of the group by the males.

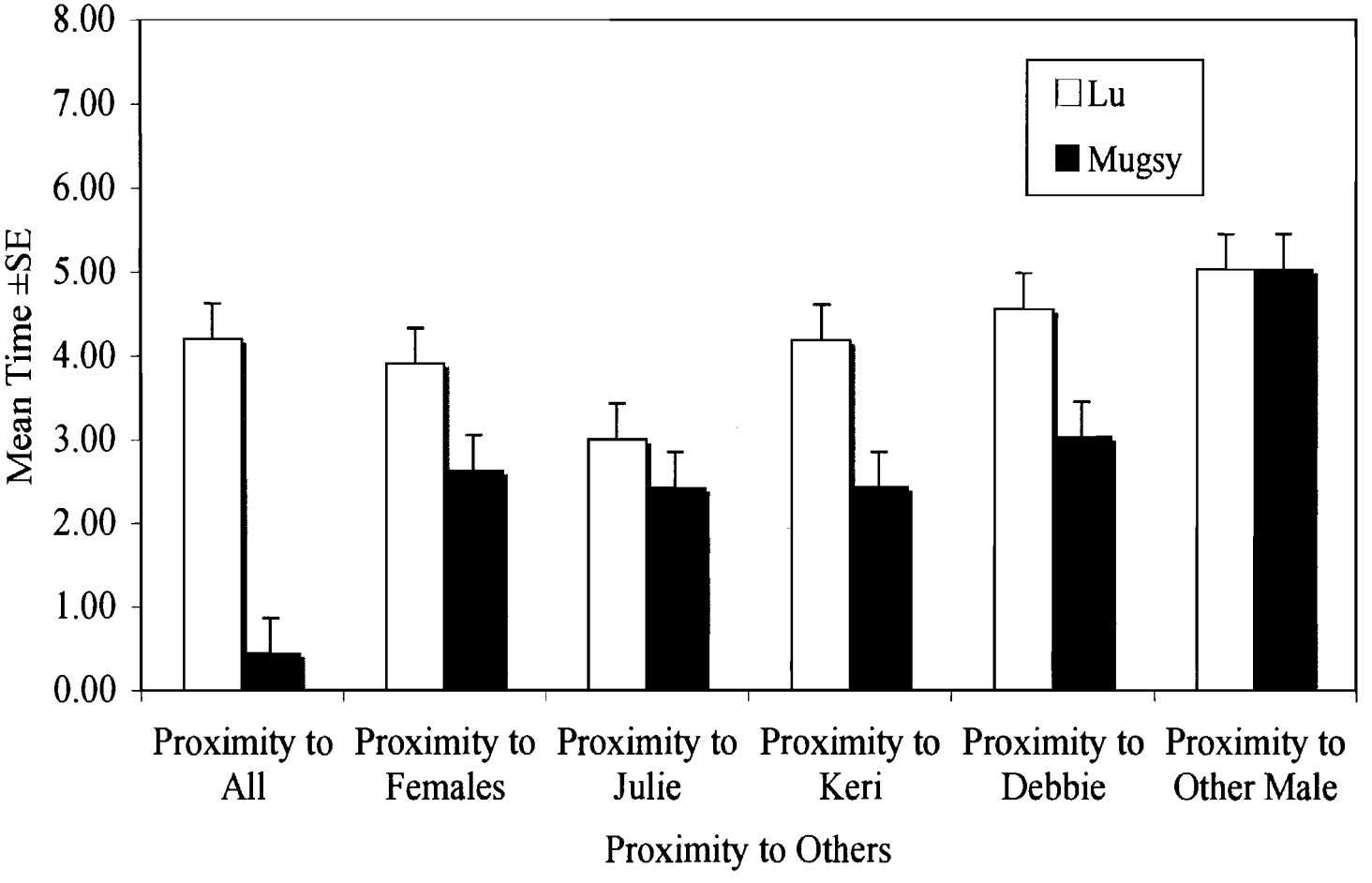

Figure 7. Mean percent time (±SE) all group members were in proximity to each male.

Table 4. The number of days each male was engaged in a grooming relationship with each female during her reproductive cycle.

	Females					
	Debbie		Julie		Kerry	
Males	#Groom Days During Swell/Swell Days	#Groom Days During Non-swell/Non-swell Days	#Groom Days During Swell/Swell Days	#Groom Days During Non-swell/Non-swell Days	#Groom Days During Swell/Swell Days	#Groom Days During Non-swell/Non-swell Days
Lu	4/27 (14.81%)	12/76 (15.79%)	1/36 (2.78%)	1/66 (1.52%)	0/11 (0%)	5/91 (5.49%)
Mugsy	3/31 (9.68%)	18/72 (25.0%)	3/34 (8.82%)	4/73 (5.48%)	0/13 (0%)	2/91 (2.20%)

Exhibit Usage

The data indicated a slightly different exhibit usage pattern for the females (Figure 8) and males (Figure 9). When the group was in the courtyard, all group members were together with no access to the outside exhibit area. Therefore, the percentage of time spent in the courtyard was nearly equal for all members. The females of the group tended to spend most of their time in area three near the second viewing window, followed by area one which is located near the first viewing area, except for Kerry who spent slightly more time in area four. Then area four located near the courtyard was the next preferred area for the females. The females spent less than 2% of their visible time in areas two, five, six, and seven. The males tended to distribute their time mostly between area one and area three (the two on-exhibit viewing areas), followed by area four, then five. The males spent less than 1% of their visible time in areas two, six, and seven.

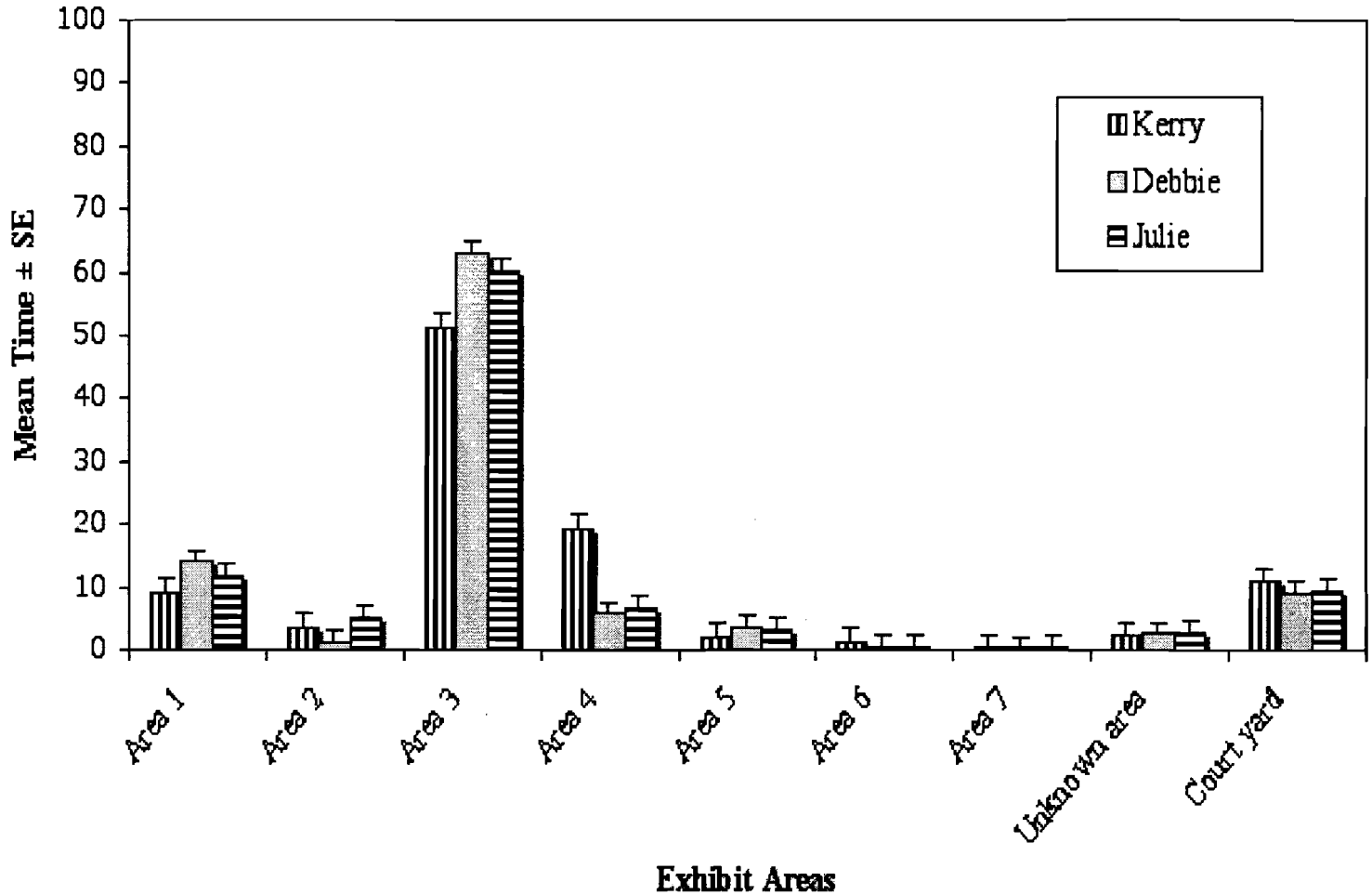

Figure 8. Mean percent time (±SE) each female spent in delineated exhibit areas.

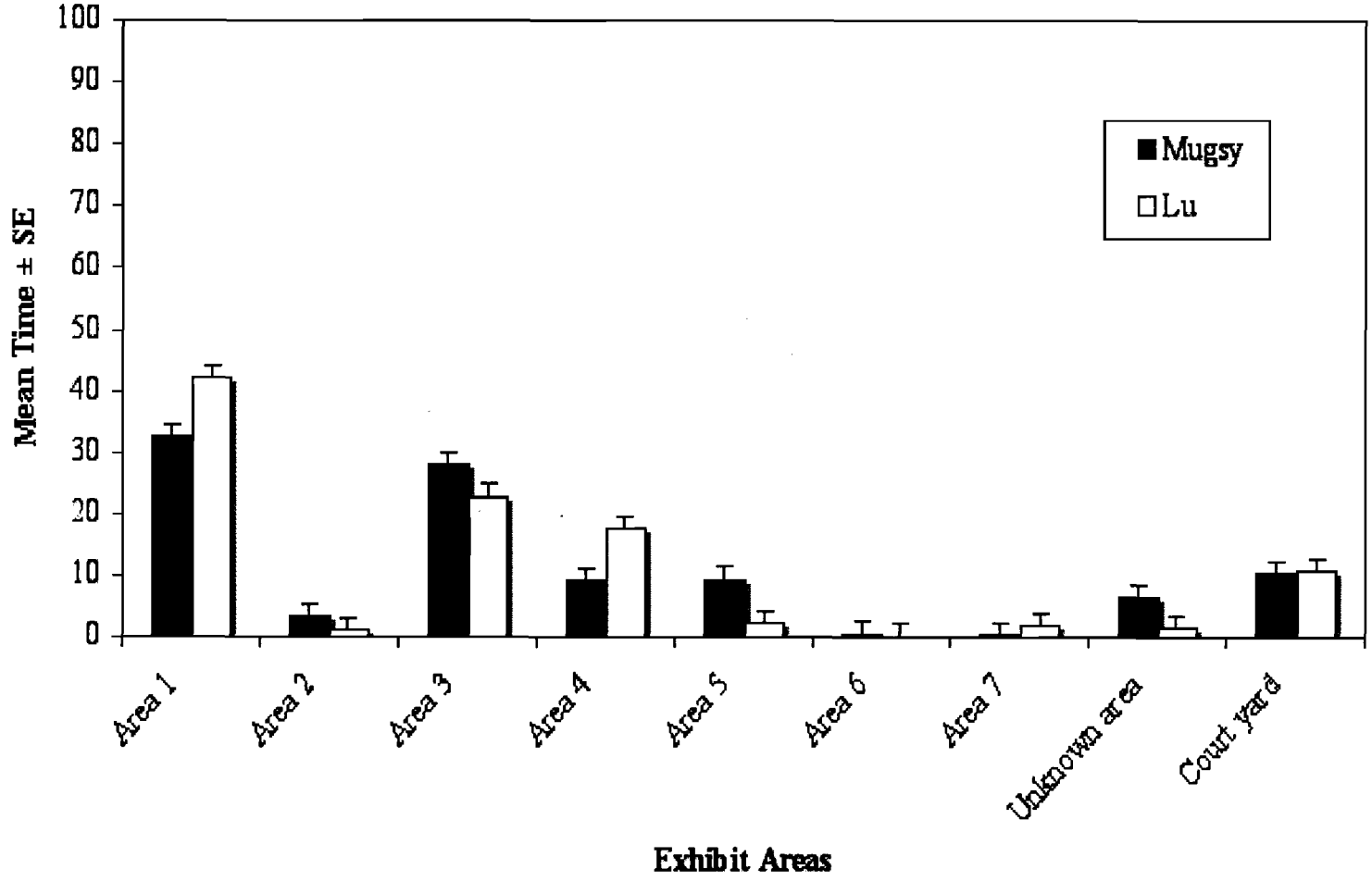

Figure 9. Mean percent time (±SE) each male spent in delineated exhibit areas.

CHAPTER IV

DISCUSSION

Overall Behavior

During the research study, the group remained in a stable state, in which no aggression or status striving behaviors were observed. Overall activity levels were low for all members of the group, with stationary behavior comprising 50% or greater of each focal animal's observation time. There were slight variations in each individual's behavior, which can be attributed to individual personality differences. For example, Mugsy was observed traveling more than others and was the only member to exhibit rocking, Lu was observed sitting stationary for 68% of the observable time, and Kerry groomed the most, particularly her mother.

In the wild, male chimpanzees tend to be more gregarious and are often observed grooming each other, whereas females are less sociable, spending the majority of their time with their offspring (Goodall, 1986). The Knoxville Zoo group deviated from this standard in that the females were more gregarious and groomed more often than the males. This is likely attributable to the unique group composition. Debbie and Kerry have maintained a strong mother-daughter bond over the years and Julie exhibited a clear preference for associating with the other females rather than the males. The cohesiveness of the females may have resulted from the fact that captivity limited the mature females' (Kerry and Julie) ability to disperse, independently travel, and start families of their own. During late adolescence, females visit and/or transfer into neighboring communities (Nishida, 1979; Goodall, 1986). A male chimpanzee changes his association focus from his mother to adult males during adolescence (Pusey, 1978;

Pusey, 1990). The lack of gregariousness of the males could have been due to the lack of adult males with which to associate. These two males lack the opportunity to develop their position in an adult male-male network. Nishsida (1979) characterized the adult male network as one of the most important characteristics of the chimpanzee unit-group (community). Captive adult males have demonstrated a similar association preference for other adult males as their wild counterparts. Fitch et al. (1989) believes that because adult males exhibit this clear preference for other adult males as association/grooming partners, providing them with opportunity to express these behaviors in captivity contributes to the "well-being" of an individual.

Adolescent Male and Dominance Behavior

Based on previous studies, the males should have been attempting to dominate the females, exhibiting agonistic behaviors towards them and towards each, and exhibiting sexual behaviors. In the wild, males begin systematically working their way into the dominance hierarchy around age 8-10, first by dominating females and low ranking males (Goodall, 1986), and throughout adolescence increase frequency and level of aggression (Goodall, 1986; Kraemer et al., 1982; Nadler et al., 1987; Pusey 1978). Adolescent males have been described as having a preoccupation with elevating their status in their community; however, these particular males under these captive conditions did not demonstrate this. There was a lack of observable overt dominant and submissive behaviors during the course of this study.

There are several possible explanations for why the males did not behave as expected for their age. It is possible that early hand-rearing had an impact on the development of sexual and status striving behavior. The males also lacked male role

models in which to observe displays, agonistic and sexual behaviors. Stevenson and Black's (1988) research on human males with paternal absence and sex-role development showed few generalizable differences between father-present and father-absent males. Stevenson and Black (1988) did find that preschool age father-absent males did not demonstrate stereotypical behavior and were less masculine; however, older father-absent boys did demonstrate stereotypical male behavior, particularly aggression. Similarly, in the Israeli Kibbutz (collective settlements) where children are communally peer-reared by a female nurse-caregiver, young males have difficulty in identifying with adult male role models, yet as they get older they become clearer about their sexual identity (Spiro, 1958). Research on captive chimpanzee males and human males are not directly comparable due to additional variables that can affect human male sex-role development such as socio-economic status, race, presence of non-paternal male role models, and sex of older siblings.

Alternately, because the males were infants when introduced to the group, they may view the females as their family group and not have any sexual interest in them. Pusey (1978; 1980) found that copulation rates were extremely infrequent between individuals that had a close relationship while both were immature. High association during early stages of life resulted in reduced sexual activity. This may be an important mechanism in preventing inbreeding in the community. Pusey (1980) reported during a female's first estrous cycle, she becomes attracted to unfamiliar males, which often leads to a change in her range. Humans have also demonstrated that peer-reared children display little sexual interest towards each other. In Israeli Kibbutzs, the second-generation children, born and bred in the same Kibbutz (peer-group) do not marry as

adults (Talmon, 1964). When asked why, they self reported that their lack of sexual interest was due to "familiarity" (Talmon, 1964). McCabe's (1983) study of the Arab FBD (father's brother's daughter) marriages and Wolf and Huang's (1980) study of the Taiwanese *sim-pua* (baby girl adopted by her future husbands family) have both demonstrated that familiarity leads to reduced sexual interest, more divorces, and few children. Shepher (1981) suggests that the phenomenon of sexual disinterest among those reared together results from an epigenetic rule that seeks to prevent inbreeding.

Long-term group stability for some captive groups has also been indicated as leading to reduce levels of sexual behavior (Coe et al., 1979; Bloodsmith et al., 1991). Bloodsmith et al. (1991) hypothesized that the notable reduction in sexual behavior may be a result of familiarity and sexual "boredom". Males who become sexually "bored", not only exhibit reduced breeding performance but lack intermale competition for estrous females. The Knoxville Zoo's group membership has remained stable since the males were introduced as infants and neither male has demonstrated intermale competition for the females.

Goodall (1986) found in wild chimpanzee that adolescent males occasionally would follow, imitate, and groom adult males and that the adult male association partners occasionally supported those adolescents. Adult males would also occasionally show aggression towards adolescent males, which teaches the younger males about the male temperament, how to avoid conflict and raise status in the dominance hierarchy (Goodall, 1986). Therefore, experience and observational learning play an important role in the development of appropriate aggressive and submissive behavioral patterns. In addition to aiding in the molding of social behavior, a competent adult male will be an effective ally

when defending the community range and resources. Since males collectively patrol and defend a territory, the development of social bonds is crucial for community protection and survival.

In captivity, adult males have also demonstrated frequent affiliative relationships with immature members of the group (Bloodsmith, 1989). By housing individuals of varying age and sex, an environment is created that has greater social complexity and increases the opportunity to interact with a variety of individuals. Immature chimpanzees can benefit from affiliative relationships with adult males, which will aid them in learning the social mechanisms that will allow them to integrate successfully into the social group and develop appropriate adult behaviors.

There are definite variations in chimpanzee personalities and degrees of sociability. The males of this study may not have been motivated to exert dominance over one another or the females during the study period. Goodall (1986) describes chimpanzee social tendencies as being inherited and developed through social interactions. Social interactions are affected by the availability of peers to play with and the type of that play. Early exposure or lack of exposure to a variety of males and females of varying ages and rank leads to the development of particular social tendencies in an individual. In the wild, certain male individuals devote more time and energy to bettering their status and ascending the social ranks than others (Riss and Goodall, 1977). Goodall (1986) found that the personality of the mothers and their sociability affected the level of aggression in her infant. An infant with a high-ranking social mother has more opportunity to interact with other infants, gradually building confidence as he tests his aggression. He can push the limits of his skills because his mother is likely to back him

up if the altercation gets serious. Throughout a males' life, regardless of his status, rank generally follows a curve pattern over his lifetime, where he will rise gradually from low rank in adolescence to his physical prime in adulthood, then decline in status as he ages and his physical strength weakens (Riss and Goodall, 1977).

Mugsy and Lu did not have normal infant socialization or the opportunity confidently test their aggression, which may have led to their lack of observable aggression towards each other and the females of the group during the study period. Bloodsmith et al. (1991) found that peer-reared chimpanzee show lower levels of dominance and activity. These two males may not be motivated to elevate their status, which may indicate that this group is a good candidate for introducing another male individual with more dominant tendencies. An adult male may be able provide these males with a role model that could help them develop more appropriate adult male behaviors that are observed in multi-male/multi-female groups. Wounding aggression occurs most often when females are in swell (Alford et al., 1995); however, since Mugsy and Lu have shown little interest in the females during their reproductive cycle, they may not demonstrate intermale competition or aggression towards a new male when the females are in swell.

Group Hierarchy

An analysis of grooming distribution among the group members helped determine the group's dominance hierarchy. Research has shown that grooming is directed up the hierarchy. The data suggested that the overall dominance hierarchy corresponded with the informal observations of the Great Apes Department, which was as follows: Debbie> Kerry> Julie> Lu> Mugsy. The females were closely bonded and could form a strong

coalition against the males, which may have also contributed to the males' lack of attempts to dominate them. Chimpanzees, in the wild and captivity, have demonstrated social awareness, a complex mental process in which an individual has the capacity to perceive social relationships between others and himself, thereby forming a concept of complex relationships which will dictate his or her behavior (de Waal, 1998; Goodall, 1986). The males of this study could have been exercising social awareness by applying their knowledge that the females have a strong coalition and that an attempt to dominate one could result in a hostile attack by all three. Debbie has continued to maintain her dominance position over the years due to her age and support of her daughter. Kerry and Julie groomed each other in nearly equal amounts; however, Kerry is considered dominant over Julie because of the alliance she has with her mother. Among the males, Lu received more grooming and Mugsy was a groomer more often, suggesting Lu has a higher rank.

Next Alpha Individual

Once Debbie is unable to defend her alpha position, one of the males will assume the dominant role. The next candidate for the alpha position was analyzed by looking at how the group distributed grooming between the males, how the males distributed grooming to other members, and the amount of time the males spent in proximity to others. The only significant difference between the males was that Mugsy distributed more grooming to others than Lu. Lu also received more grooming and was in proximity to others more often; however, this difference was not significantly more than Mugsy. Based on the theory that those who groom more than they receive tend not to be dominant, we can predict that Lu will be our next alpha male. Members who are more

frequently in proximity have the propensity for choosing one another as an association partners (Hayaki, 1988) and show high rates of alliance formation (Seyfarth, 1980). The research data indicated that Lu has an advantage over Mugsy, such that in the event of an agonistic encounter the females are likely to give support to Lu. Therefore, with the support of the females, his potential for rising in rank increases. Research on the group in 1996 and 1997 showed that Mugsy had established cohesive bonds with the females, where Lu had not (Seyfert, 1997). Chimpanzee relationships are often dynamic and partnerships and alliances can change over time. As the males continue to mature, female preference could fluctuate, which may contribute to changes in alpha status.

As an additional note, both males exhibited behaviors that are a result of their early hand-rearing process, which may have interfered in the development or expression of dominance behaviors characteristic of their age and sex. Fritz and Fritz (1985) in their observations of hand-reared chimpanzees, reported that the first 12 months of life are critical for learning appropriate sexual and social behavior and those that exhibit stereotypical rocking, never achieve dominant status. They suggest that the expression of rocking reflects a disrupted maturational process, which then is likely to give rise to additional social and motor problems as the individual matures. Mugsy rocks only when in the courtyard area of the exhibit; however, this may be an indicator that his social skills have been impacted as a result of hand-rearing without another conspecific during the first year of his life. Human caregivers unfortunately cannot replicate the same amount of stimulation a mother-reared individual receives, which has the potential to affect certain developmental processes in young chimpanzees. Personal communications with the Knoxville Zoo staff revealed that Lu has an unusually strong bond with his

human caregivers and has on several occasions given up the opportunity to go outside with the group members to stay near one of his caregivers in the Great Apes building. He also has been observed to interact with human visitors near the viewing areas and even attempts to groom through the viewing glass. Lu's unusual bond to humans can directly be related to the fact that humans were his primary attachment figure and source of security when he was being hand-reared, which has had a long lasting effect on his relationship with them.

Grooming and Female Reproductive Condition

Female sociability changes during the different stages of their reproductive cycle, where sociability increases during estrous (Goodall 1986, Bloodsmith et al., 1991). Increased sociability with the males was not observed for the Knoxville Zoo females. Since sexual behavior was not observed during the study period, grooming was used as a measure of interest during times of swell. The males and females did not exhibit a greater interest in grooming with each other during the times the females were exhibiting a sexual swelling. In the wild, males tend to associate with females more when they are in estrous (Goodall, 1986). Mugsy and Lu did not have the opportunity during their maturational period to observe appropriate adult male behavior towards females during estrous, which could explain their lack in interest in the females at this time. Kramer et al. (1982) found adolescence coincides with a peak in sexual behavior in captive mixed-sex social groups. In the wild, there appears to be a reduced level of sexual behavior in adolescence, which is believed to be a result of adult males inhibiting adolescent male copulation (Pusey, 1990). In this study, there were no adult males to inhibit copulation, yet sexual interactions were not observed. As stated previously, it is possible that

reduced sexual interest, breeding performance, and intermale competition can result from long periods of group stability and the males' having had a close relationship with the females while immature. Bloodsmith et al. (1994) found that individuals born into complex breeding groups developed levels of sex and submissive behaviors that closely resembled those seen in studies on free-ranging chimpanzees. Essentially, a complex rearing environment promotes the development of appropriate species-typical social behavior. Adult group members may be critical to elicit normal levels sexual interactions and force submission behaviors, thus, explaining why peer-reared individuals deviate from the norm (Bloodsmith et al., 1994).

Exhibit Usage

The fission-fusion social structure of wild chimpanzees was reflected by the exhibit usage patterns of the current study group. The 5058m^2 naturalistic exhibit afforded the group the opportunity to be in separate areas of the exhibit or come together and socialize. The preferred areas of the exhibit were near the two viewing areas, which provided the public with an excellent opportunity to see chimpanzees interacting in a naturalistic enclosure. The males and females tended to spend their time in separate areas of the exhibit; however, during feedings the group would come together and feed. The group had also been observed traveling together from one end of the exhibit to the other. During exceptionally hot days, the group would spend a great deal of time in the shade near the rear of the exhibit, which made observations and public viewing difficult.

Conclusion

The aim of this study was to elucidate the behavior of the Knoxville Zoo chimpanzee group. This study has provided some insight into this unique group's social

behavior and dominance hierarchy. This captive group of chimpanzees exhibited a stable social organization. We can only speculate why the adolescent males did not exhibit behaviors characteristic of their age and sex. Since animal transfers are frequent occurrences for zoos, knowledge of these males' and females' behavior will aid managers in predicting how a new individual can be successfully integrated. This information also provides valuable data for future analyses on this group's social dynamics.

More observation time is required to elucidate which male will become the next alpha individual. Observation times were limited to the times when all group members were exhibited and could not include times when they were off exhibit in their dens. In addition, visibility was also limited to three viewing areas and when any focal animal was out of sight for greater than 10-minutes, the observation session was cancelled. Increasing observation time while the animals are on and off-exhibit, will contribute a larger body of data for analyses to offset the amount of time they spend stationary.

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APPENDICES

APPENDIX A

ETHOGRAM FOR

Pan troglodytes

AGST -Agonistic behavior –state

Definition: Broad term used to define non-friendly interactions. It is usually accompanied by pilo-erection in the aggressor. An agonistic state is a series or "package" of aggressive behaviors that occur in rapid succession and extend for periods of variable duration. An agonistic state can include any rapid combination of aggressive events.

Examples: These agonistic "attacks" can include such behaviors as slapping, kicking, biting, hitting, chasing, and rock/feces throwing.

Special Notes: An agonistic state should not be confused with a display, which may sometimes be an antecedent to an agonistic event or state.

Outcomes to agonistic behavior (usually seen in the target chimpanzee) can include screaming, pilo-erections, open and closed mouth grins, agonistic behavior, and/or submissive behaviors such as crouching and presenting to the agonistic individual.

AGEV -Agonistic behavior -event

Definition: An agonistic event is a single aggressive act, which must be separate from another aggressive act by more than 3 seconds.

Examples: An aggressive act/event can include a slap, kick, hit, bite, or throw of an object (including feces).

AC -Approach chimpanzee -event

Definition: Approach chimpanzee (AC) consists of locomotion of the focal chimpanzee toward another individual. The pace of an approach may vary from a slow walk to a full run.

Special Notes: AC should be scored when the focal comes within 1 meter of the target individual.

AFILIATIVE – Affinitive – event

Definition: Friendly/non-aggressive physical contact that is not Grooming, Buddywalk, Embrace, or Social Play. Appear to be acts of reassurance.

Examples: Kiss, touching of arm, hand, head, foot, leg, torso, or genitals.

ANGN –Anogenital inspection/manipulation -state

Definition: Visual, oral, or manual inspection of the anogenital region. May be social or self-directed. With anogenital inspection (ANGN), the chimpanzee often puts its face very close to the anogenital region of another and often pushes its lips forward, possibly sniffing. (Berdecio and Nash, 1981).

Special Notes: ANGN should not be confused with scratching, masturbation, or manipulation of anus to obtain feces.

AVOID -Avoid -event

Definition: One animal actively evades physical contact or interaction with another animal. This is usually performed by quick locomotion away from the directly approaching chimpanzee.

BEG -Beg -event

Definition: A gesture where the chimpanzee reaches an outstretched hand to another or puts its lips to an object of interest which may be in the mouth, hand, or foot of the possessor.

Examples: This behavior is usually seen when another individual has some object of interest such as food or a toy; it may also be seen as an antecedent to the approach of another, or to a grooming session.

Special Notes: Begging may not be successful and is sometimes followed or accompanied by whimpering and tantrums.

EMB- Embrace -state

Definition: Two individuals will put one or both arms around the other. Positions may be ventral-ventral, lateral, or dorsal-ventral.

DISPLAY -Display -state

Definition: A display is a series of locomotor movements, facial expressions, and vocalizations, which gradually increase in intensity and may sometimes culminate into an agonistic event or state, or may gradually subside and end with rocking, grooming, close proximity to another, etc.

Examples: The displayer may move in a slow rhythmic gait and then may run at a moderate or very fast speed. Often the chimpanzee will run bipedally, have a pilo-erection, and sway its body and arms from side-to-side. Behavioral patterns that accompany a display include any or all of the following: throwing, branch dragging, branch swaying, slapping, stamping, drumming, raking and flailing. The displayer may hold a branch, stick, or handful of vegetation in one hand, which it may thrash or wave at

another. The lips of the chimpanzee may be compressed and he may emit loud pant hoots.

Special Notes: This behavior is typically seen in, but not restricted to males. May result in agonistic interactions of some kind.

FEAR -Fear -state

Definition: Chimpanzee displays behaviors that appear to be of extreme anxiety due to another individual(s) or to a new or stressful situation.

Examples: The chimpanzee may crouch, display an open or closed mouth grin, scream, run away from the source of uneasiness, or toward it (in the case of an aggressor), or the frightened chimpanzee may seek out comfort from another individual (which would be scored as an approach).

FOLLOW -Follow -state

Definition: The focal animal travels behind another individual. The lead chimpanzee and the follower usually travel quadrupedally, but sometimes they may brachiate. The pace of this behavior is most often slow and relaxed, but may be moderate.

Special Notes: The focal chimpanzee may never attempt an approach, but may simply walk behind the target individual at the pace moderated by the target. Follow (FO) should not be confused an agonistic chase where the target animal may be screaming, running, looking over it's shoulder, and actively attempting to avoid the aggressor; should also not be confused with playful interactions which are often at a much quicker pace and where one or both of the individuals may be displaying a play face.

FRU/TAN –Frustration/Tantrum -state

Definition: Frustration: Chimpanzee displays behaviors of irritation or mild distress in response to being denied something of interest or in response to displacement or aggression by a more high-ranking individual. Tantrum: This behavior is topographically and functionally similar to frustration only more intense.

Examples: If the animal is unsuccessful in receiving an object after begging or is displaced by a more high-ranking individual, frustration (FRU) may be indicated by the chimpanzee shaking it's hands or the cage, banging the cage, and displaying an open or closed mouth grin. With a tantrum (TAN), the chimpanzee may scream loudly, leap up and down, fling its arms, shake its hands, place its face on the ground, hug a tree, or itself, and display an open or closed mouth grin.

Both behaviors are typical of infants as seen when mother denies suckling, refuses to allow the infant to ride on her back, share her food, etc. Older animals may also display these behaviors as indicated above.

Special Notes: The intense screaming which often accompanies a tantrum may result in glottal cramps which sound very much like coughs and gags.

GROOM/OTHER GR –Groom/Other Groom -state

Definition: A social or solitary activity where the chimpanzee picks through the hair, searching for and/or removing debris from the body. Grooming is often accompanied by teeth clacking or lip smacking. Grooming (GR) is performed by the focal animal and Other Groom (OGR) is performed by another chimpanzee to the focal animal.

Special Notes: Grooming should not be confused with scratching; grooming is a more focused behavior.

LOC PLAY -Locomotor Play -state

Definition: LOCPL is categorized by repeated or nonstandard locomotor patterns which are not the typical methods of travel (i.e., quadrupedal, bipedal, or brachial movement) as seen when the individual is traveling from point A to point B. This behavior is often seen with a play face.

Examples: The individual may roll head over tail, turn pirouettes, swing back and forth on a rope or from the enclosure.

Special Notes: Movement should seem voluntary and deliberate rather than just idle, residual, and/or very low intensity movement as seen, for example, when an individual is hanging from the top of the enclosure after brachiating and the legs are lightly moving back and forth. In this case, the behavior should be stored as stationary STA.

MT/TH –Mount/Thrust -state

Definition: Mount: Chimpanzee will place part of its ventral surface in contact with the dorsal surface of another. The mounter usually leans forward over the other. Thrust: Chimpanzee performs rhythmic back and forth movements of the pelvis (eg., copulatory movements) on another individual or an object.

Special Notes: To distinguish from Buddywalking, only score this behavior when followed by thrusting.

NV -Not visible

Definition: Chimpanzee is out of sight of the observer.

OBM -Object manipulation -state

Definition: To actively operate an object with the hands or feet, displaying mechanical skills. This behavior serves a variety of functions, but in every case involves the active utilization and/or control of an object.

Examples: Object manipulation may be seen when a chimpanzee uses a tool to retrieve food, throws straw in the air, bangs on a rock or tub, catches urine or feces with the hands or feet, runs it's fingers/toes through a water puddle, rolls a ball or barrel, etc.

Special Notes: Object manipulation may occur with a play face. If OBM is accompanied by a play face, please note in comments.

OCA -Other chimpanzee approach -event

Definition: The locomotion of an individual chimpanzee toward the focal chimpanzee. The pace of an OCA may vary from a slow walk to a full run. (Berdecio and Nash, 1981)

Special Notes: This behavior is topographically similar to Approach Chimpanzee (AC), but the focal is a passive recipient rather than directing the action.

OCA should be scored when the chimpanzee approaches within 1 meter of the focal.

OTHER -Other

Definition: Any solitary or social behavior other than that listed, including eating, defecating, and urinating.

Special Notes: When Other (OT) occurs, the coder should note the behavior in comments.

PRESENT -Present -event

Definition: Chimpanzee turns so that anogenital region is facing another.

Examples: Presenting may be used as a submissive gesture, as a copulatory invitation, or as an antecedent to buddywalking or an embrace.

Special Notes: This behavior is sometimes referred to as rump-turning.

PROX -Proximity -state

Definition: The focal chimpanzee is within lm of another chimpanzee and neither is traveling, but no obvious social interactions are occurring between the pair.

Examples: Two chimpanzees are sitting side by side, one is asleep and the other is grooming himself; or one is digging in the dirt (OBM) and the other is rocking; or the focal is sitting next to a grooming pair, etc.

Special Notes: Both the focal and the other individual should be engaged in separate activities for this category to be scored. PROX may be scored with behaviors like solitary grooming, object manipulation, stationary, fear, etc. Basically, any behavior that is not a

social interaction and takes place in one location. The focal animal may be in proximity to another pair that is engaged in social activity, as in the last example given above.

SOC PLAY -Social play -state

Definition: Non-aggressive interactions between two or more individuals that is often accompanied by a play face and raspy pants.

Examples: Social play (SOCPL) can include one or a combination of tickling, wrestling, biting, sparring, chasing, butting, kicking, dragging, etc.

Special Notes: Should not be confused with AGST which is an aggressive interaction where one or both animals may be screaming, displaying open or closed-mouth grins and inflicting injury on another.

ROCK -Rock –state

Definition: Rhythmic movements of the body, either side-to-side or rostrally- caudally.

STATIONARY -Stationary -state

Definition: Animal is idle and in one location but may be lightly swaying legs, may be asleep or awake, and may be in Proximity to another.

TRAVEL -Travel -state

Definition: A deliberate means for moving from point A to point B including quadrupedal, bipedal or brachial locomotor movements.

Examples: Animal may walk, run, or swing arm-over-arm on vines or cage tops to get to a destination.

Special Notes: Should NOT be confused with LOCPL which involves unique or repetitive locomotor movements which are not standard or energetically wasteful when considered for traveling, like turning flips or jumping up and down.

WATCH -Watch -state

Definition: Close visual inspection as indicated by obvious orientation of the head toward an object or individual or by placing the head very close to the object of interest.

A mutually exclusive category except for the possible occurrence with PROX

FACIAL EXPRESSIONS

*Definitions of facial expressions are from (Berdecio and Nash, 1981). Some of the definitions may have been slightly modified to be more applicable to the study group.

Normal, relaxed face.

Definition: With this expression, all facial features are in a neutral position. The eyes are open and the brows are relaxed or slightly raised. The mouth is relaxed and may be closed or slightly parted. The lower lip may hang down.

Closed-mouth grin.

Definition: With this facial expression, the brows are often pulled together, but may be in a normal position, or slightly raised. The mouth is closed and comers are fully withdrawn. The teeth are clenched and exposed. The gums of the mouth are also often exposed. This expression is a silent display with no accompanying vocalizations.

Special Notes: see Special Notes below

Open-mouth grin.

Definition: This expression is similar to the closed-mouth grin, but the mouth is open with the comers fully retracted. All of the teeth and very often the gums are exposed. This facial expression may be accompanied by screaming or whimpering sounds.

Special Notes: Both the closed-mouth grin and open-mouth grin are observed in stressful or fearful situations.

Hoot face.

Definition: With this expression, the eyes are wide and the browns are in a normal or raised position. The mouth is closed with the corners relaxed. The lips are pushed forward and curved outward at the center, creating a circular appearance of the lips. This facial expression always occurs with a low hooting vocalization that often escalates in intensity.

Special Notes: Hooting occurs most often as a response to a sudden visual or auditory stimulus or to changes in surroundings. This expression is also seen during displays.

Play face.

Definition: With this expression, the mouth is moderately to widely open; the mouth corners are pulled up and may be slightly curved. The upper teeth may be fully or partially concealed; the lower lip is retracted and the lower teeth exposed. Often accompanied by rapid, rhythmic breathing which mayor may not be vocalized.

Special Notes: Seen during playful situations.

APPENDIX B

Chimp _____ _____ _____ __ **Date**_____ _____ _____ ___

Enclosure																Enclosure												
State	0	15	30	45	1	15	30	45	2	15	30	45	3	15	30		45	4	15	30	45	5	15	30	45	6	15	30	45
Groom																Groom												
Other Gr.																Other Gr.												
Follow																Follow												
AgSt																AgSt												
Display																Display												
Stationary																Stationary												
Travel																Travel												
Watch																Watch												
Fru/Tan																Fru/Tan												
Loc.Play																Loc.Play												
NV																NV												
ObM																ObM												
Other																Other												
Prox.																Prox.												
Soc. Play																Soc. Play												
Rock																Rock												
Fear																Fear												
ANGN																ANGN												
Mt/Th.																Mt/Th												
Closed-Grin																Closed-Grin												
Open-Grin																Open-Grin												
Event	0	15	30	45	1	15	30	45	2	15	30	45	3	15	30	Event	45	4	15	30	45	5	15	30	45	6	15	30	45
AgEv																AgEv												
Beg																Beg												
AC																AC												
OCA																OCA												
Present																Present												
Avoid																Avoid												
Affiliative																Affiliative												
Fear																Fear												
Emb.																Emb.												

Enclosure																Enclosure												
State	7	15	30	45	8	15	30	45	9	15	30	45	10	15	30	State	45	11	15	30	45	12	15	30	45	13	15	30	45
Groom																Groom												
Other Gr.																Other Gr.												
Follow																Follow												
AgSt																AgSt												
Display																Display												
Stationary																Stationary												
Travel																Travel												
Watch																Watch												
Fru/Tan																Fru/Tan												
Loc.Play																Loc.Play												
NV																NV												
ObM																ObM												
Other																Other												
Prox.																Prox.												
Soc. Play																Soc. Play												
Rock																Rock												
Fear																Fear												
ANGN																ANGN												
Mt/Th.																Mt/Th												
Closed-Grin																Closed-Grin												
Open-Grin																Open-Grin												
Event	7	15	30	45	8	15	30	45	9	15	30	45	10	15	30	Event	45	11	15	30	45	12	15	30	45	13	15	30	45
AgEv																AgEv												
Beg																Beg												
AC																AC												
OCA																OCA												
Present																Present												
Avoid																Avoid												
Affiliative																Affiliative												
Fear																Fear												
Emb.																Emb.												

Enclosure																Enclosure									
State	14	15	30	45	**15**	15	30	45	**16**	15	30	45	**17**	15	30	State	45	**18**	15	30	45	**19**	15	30	45
Groom																Groom									
Other Gr.																Other Gr.									
Follow																Follow									
AgSt																AgSt									
Display																Display									
Stationary																Stationary									
Travel																Travel									
Watch																Watch									
Fru/Tan																Fru/Tan									
Loc.Play																Loc.Play									
NV																NV									
ObM																ObM									
Other																Other									
Prox.																Prox.									
Soc. Play																Soc. Play									
Rock																Rock									
Fear																Fear									
ANGN																ANGN									
Mt/Th.																Mt/Th									
Closed-Grin																Closed-Grin									
Open-Grin																Open-Grin									
Event	14	15	30	45	**15**	15	30	45	**16**	15	30	45	**17**	15	30	Event	45	**18**	15	30	45	**19**	15	30	45
AgEv																AgEv									
Beg																Beg									
AC																AC									
OCA																OCA									
Present																Present									
Avoid																Avoid									
Affiliative																Affiliative									
Fear																Fear									
Emb.																Emb.									

Chimp: _____ Date: _____ Time: _____ Weather: _____

Behavior	Freq. Events	%/RateStates	Notes
Enclosure			
State			
Groom			
Other Gr.			
Follow			
AgSt			
Display			
Stationary			
Travel			
Watch			
Fru/Tan			
Loc.Play			
NV			
ObM			
Other			
Prox.			
Soc. Play			
Rock			
Fear			
ANGN			
Mt/Th			
Closed-Grin			
Open-Grin			
Event			
AgEv			
Beg			
AC			
OCA			
Present			
Avoid			
Affiliative			
Fear			
Emb.			

Table A1. Mean percent time each focal chimpanzee spent in general state behaviors for greater than 1% of visible time.

	State Behaviors							
Focal Animal	**Groom**	**Receiving Grooming**	**Stationary**	**Travel**	**Watch**	**ObM**	**Other**	**Rock**
Kerry	**33.05**	**13.22**	**49.88**	**8.80**	**0.32**	**3.14**	**4.33**	**0.03**
Debbie	**24.63**	**18.49**	**64.24**	**4.99**	**0.59**	**1.02**	**3.50**	**0.03**
Julie	**18.75**	**5.74**	**57.27**	**10.72**	**0.57**	**2.67**	**9.56**	**0.00**
Mugsy	**11.96**	**3.69**	**57.65**	**14.13**	**1.92**	**2.36**	**8.86**	**1.90**
Lu	**4.12**	**4.07**	**67.98**	**9.06**	**2.35**	**4.02**	**11.72**	**0.00**

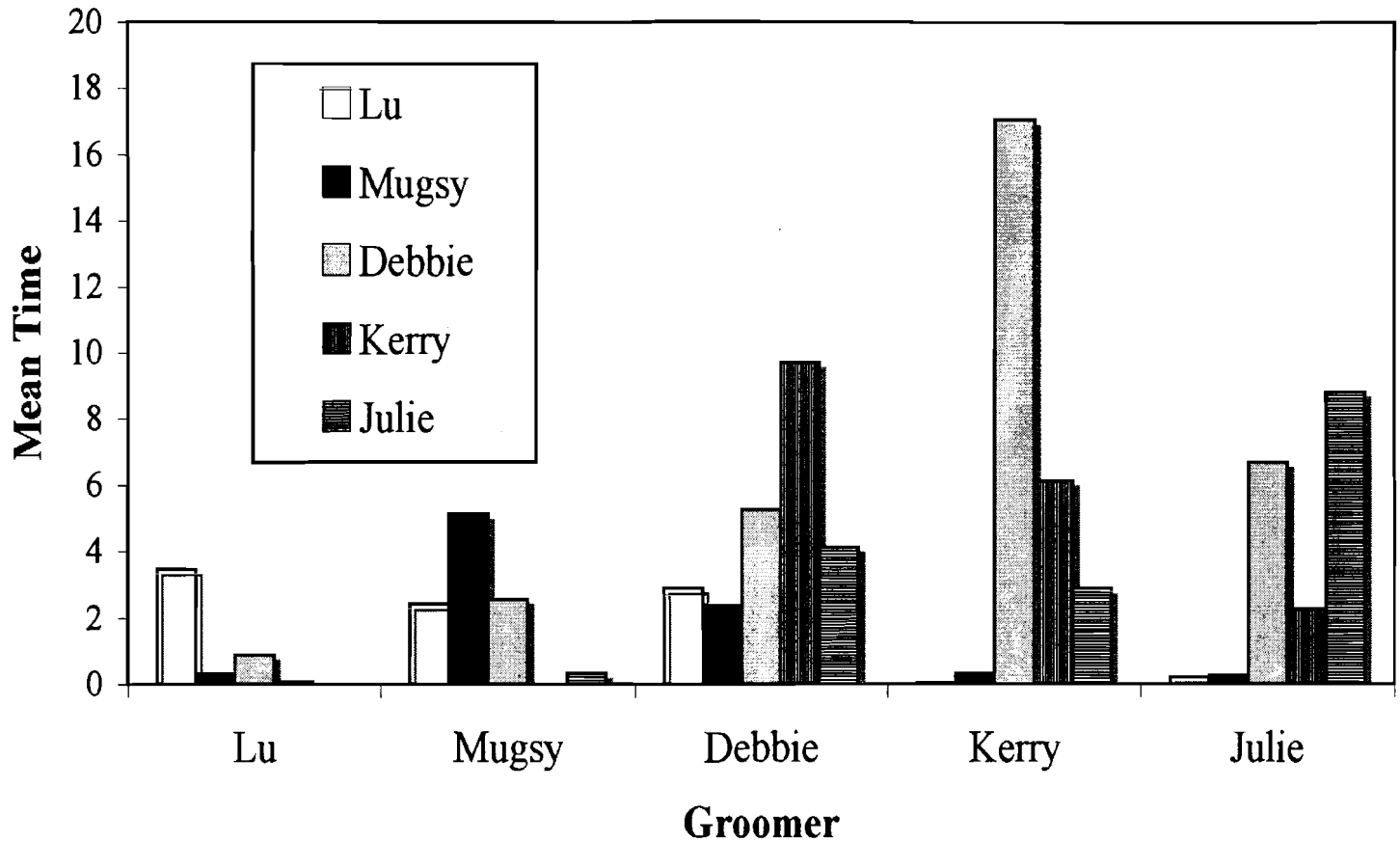

Figure A1. Mean percent time each chimpanzee spent grooming themselves and other members of the group.

Table A2. Mean percent time grooming was given to each male by other members of the group.

	Males		
Grooming By	**Lu**	**Mugsy**	**p-value**
By All	**1.40**	**0.80**	**0.628**
By Females	**1.04**	**0.98**	**0.533**
By Julie	**0.21**	**0.27**	**0.154**
By Keri	**0.03**	**0.32**	**0.429**
By Debbie	**2.89**	**2.35**	**0.734**
By Other Male	**2.42**	**0.30**	**0.07**

***Indicates significance at alpha level 0.05**

Table A3. Mean percent time grooming was given to other members of the group by the males.

	Males		
Grooming To	**Lu**	**Mugsy**	**p-value**
To All	**0.31**	**1.34**	**0.001***
To Females	**0.31**	**0.96**	**0.007***
To Self	**3.48**	**5.13**	**0.036***
To Julie	**0.00**	**0.33**	**0.043***
To Keri	**0.07**	**0.01**	**0.997**
To Debbie	**0.87**	**2.56**	**0.022***
To Other Male	**0.30**	**2.42**	**0.07**

***Indicates significance at alpha level 0.05**

Table A4. Mean percent time all group members were in proximity to each male.

	Males		
Proximity To	**Lu**	**Mugsy**	**p-value**
Proximity to All	**4.20**	**0.44**	**0.241**
Proximity to Females	**3.91**	**2.62**	**0.114**
Proximity to Julie	**3.00**	**2.42**	**0.128**
Proximity to Keri	**4.18**	**2.43**	**0.283**
Proximity to Debbie	**4.56**	**3.03**	**0.844**
Proximity to Other Male	**5.03**	**5.03**	**1**

***Indicates significance at alpha level 0.05**

VITA

Crystal Elizabeth Anderson was born in Las Vegas, Nevada on June 5, 1975. She went to grade school in Bourbonnais, Illinois and high school at Upper Dublin High School in Dresher, PA. She graduated high school in 1993. From there, she went to Saint Mary's College of Maryland and received a B.A. in Biology in 1997. Following graduation, she worked as a wildlife field technician for the Bureau of Land Management in Klamath Falls, OR and for the Pennsylvania State Game Commission, Harrisburg, PA.

Her passion for working with animals led her to graduate school at the University of Tennessee, Knoxville. She earned a M.A. degree in Psychology and focused her curriculum on Animal Behavior. Her future career goals are to continue to work in the animal field and contribute to the conservation and preservation of wildlife.